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Research Document 2004/008 | **Document de recherche 2004/008**

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Pacific Herring Spawn Disappearance and Recolonization Events

Périodes d'absence et de reprise de la fraie du hareng du Pacifique

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Ce document est disponible sur l'Internet à:

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ISSN 1499-3848 (Printed / Imprimé)
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Abstract

This is the fourth in a series of papers outlining the evidence that British Columbia herring are spatially structured and interact as a metapopulation. The purpose of this paper is to analyze the spawn time series for indications of "disappearance" and "recolonization" events. Some local communities in British Columbia (BC) believe that each bay where herring spawn contains a genetically discrete stock. Accordingly, if one of these "stocks" fails to return to spawn the implication is that some unique genetic diversity has probably been lost. The metapopulation concept provides an ecological basis for explaining that small, herring spawning aggregations can disappear for a time due to dispersal and other natural causes. And that vacant habitat will eventually be recolonized, when suitable conditions return. We analyzed the spawn time series (from 1943 to 2002) in 76 spatial "sections" where herring spawn in BC. We identified 82 spawn disappearance events, and found that 55% of the sections experienced one or more disappearance events in the last 60 years. We found that small sections experience more disappearance and recolonization events than sections with larger amounts of spawn habitat. Stray spawners from other areas recolonize vacant sections in 11 years, on average. Some sections were recolonized in less than five years; while at the other extreme, one section has not been recolonized for 35 years. Only 53 % of the recolonization attempts were successful. The high degree of straying between nearby sections explains why herring spawning aggregations at the "section" spatial-scale are so dynamic from year-to-year, and have a very low coherence. We found that 18 sections currently contain no spawn. These vacant sections have smaller amounts of spawn habitat, and a higher probability of disappearance events than occupied sections. The balance between the spawn disappearance and recolonization rates changed in Southern BC toward the end of the last "cool" climate regime. During the first half of the warm regime that followed the disappearance rate tended to be much higher than the recolonization rate, so the number of sections occupied by spawners declined. In the Northern sections, the disappearance and recolonization rates have tended to be more balanced. However, over the last 60-years when the disappearance (and recolonization) rates were higher in the South, they also tend to be higher in the North. In 34 of the 76 sections examined, there were no spawn disappearance events. These important sections contain about 85% of the total herring spawn habitat in BC, and therefore should be protected from shoreline development, pollution and other sources of habitat degradation. Loss of these habitats will almost certainly have a negative impact on the dynamics and resilience of the metapopulation.

Résumé

Ce document est le quatrième d'une série de documents qui présentent des données montrant que, par sa répartition spatiale et ses interactions, le hareng de la Colombie-Britannique (C.-B.) forme une métapopulation. Ce document vise à analyser une série chronologique pour y déceler les périodes sans reproduction et les périodes de reprise de celle-ci dans les zones de fraie. Dans certaines collectivités de la C.-B., on croit que chaque baie où le hareng fraie contient un stock génétiquement distinct. Si un de ces « stocks » ne revient pas frayer, cela signifierait probablement qu'une composante unique de la diversité génétique est perdue. Le concept de métapopulation offre une explication écologique du fait que de petits groupes de géniteurs peuvent disparaître pour un certain temps en raison de leur dispersion ou d'autres causes naturelles et que l'habitat inoccupé sera recolonisé lorsque les conditions redeviendront favorables. Nous avons analysé la série chronologique de données sur la fraie (de 1943 à 2002) dans 76 secteurs de fraie du hareng en C.-B. Nous avons relevé 82 périodes sans fraie et trouvé qu'il y a eu au moins une de ces périodes dans 55 % des secteurs depuis 60 ans. Les périodes de disparition et de reprise de la fraie étaient plus fréquents dans les petits secteurs que dans ceux contenant davantage d'habitat de fraie. En moyenne, les secteurs inoccupés sont recolonisés au bout de 11 ans par des géniteurs égarés provenant d'autres secteurs. Certains secteurs ont été recolonisés en moins de cinq ans, tandis qu'un secteur ne l'a pas été depuis 35 ans. Seulement 53 % des tentatives de recolonisation ont été réussies. Le niveau d'égarement élevé entre des secteurs avoisinants explique pourquoi les groupes de géniteurs sont si dynamiques d'une année à l'autre (à l'échelle des secteurs) et présentent une très faible cohérence. Dix-huit secteurs connaissent actuellement une période sans fraie : ils contiennent moins d'habitat de fraie et présentent une probabilité plus forte de périodes sans fraie que les secteurs occupés. Dans le sud de la C.-B., le rapport entre les taux de disparition et de reprise de la fraie a changé vers la fin du dernier régime climatique « frais ». Durant la première moitié du régime « chaud » qui a suivi, le taux de disparition était beaucoup plus élevé que le taux de recolonisation, et le nombre de secteurs occupés par des géniteurs a donc baissé. Dans les secteurs nordiques, les taux de disparition et de recolonisation tendent à être plus équilibrés. Toutefois, depuis 60 ans, lorsque les taux de disparition (et de recolonisation) sont plus élevés dans le sud, ils ont tendance à l'être aussi dans le nord. Trente-quatre des 76 secteurs étudiés n'ont connu aucune période sans fraie; ces secteurs importants contiennent environ 85 % de l'ensemble de l'habitat de fraie du hareng en C.-B. et devraient donc être protégés contre l'aménagement du littoral, la pollution et d'autres facteurs de dégradation de l'habitat. La perte de ces habitats nuirait presque sûrement à la dynamique et à résilience de la métapopulation.

Introduction

In the past decade there has been a renewed interest in studying the spatial structure of natural populations, because it is now widely recognized that most animals live and reproduce in fragmented habitats. In this context, McQuinn (1997) reviewed the ecological characteristics of Atlantic and Pacific herring and concluded that the stock structure of these species resembled a *metapopulation*. A metapopulation is simply a set of interacting, local breeding populations, which are linked by dispersal (or straying). Dispersal is important because it can have a significant effect on the production dynamics and genetic differentiation of local populations. The particular kind of heterogeneity that metapopulation ideas focus on is the largely independent dynamics of local populations in discrete habitat patches (Hanski, 1996). Metapopulation theory also recognizes that some elements of the population can disappear for a time, because of a temporary loss in the amount (or quality) of the spawning habitat, dispersal, or other factors. However, when suitable conditions return these vacant habitats can be recolonized by migrants from nearby habitats (Hanski and Simberloff 1997).

Extensive research indicates that the spawning habitat of BC herring is fragmented, and that herring disperse between these fragments both within and between stock assessment regions (Hay et al 1999). Ware et al (2000) reanalyzed a subset of the tagging data for the five, major migratory herring populations in BC. They found: 1) that these populations were linked by dispersal; 2) that the dispersal pattern matched an isolation by distance model; and 3) that the dispersal rate increased as the abundance of spawners approached the carrying capacity of the habitat. Ware and Schweigert (2001, 2002) analyzed the production and dispersal dynamics of the five major herring populations during the cool (1951-76), and subsequent warm (1977-98) climate regimes, and assimilated the results into a structured metapopulation model. Models of this form contain an explicit description of the local dynamics of the component populations, and include the effects of dispersal on population growth rates (Hanski 1996). They used the model: 1) to quantify the recruitment rates and amount of dispersal that probably occurred between the major herring populations during these two climate regimes; and 2) to assess the impact of local variations in recruitment and dispersal on the dynamics of the metapopulation. They also evaluated the resilience of the five major populations to harvesting. For more background information about the basic biology of BC herring and the history of the fishery, the reader is referred to an excellent review by Stocker (1993).

This is the fourth in a series of papers outlining the evidence that British Columbia herring are spatially structured and interact as a metapopulation. The purpose of this paper is to analyze the spawn time series for evidence of "disappearance" and "recolonization" events. A key element of metapopulation theory is that not all suitable habitats are occupied simultaneously, and that

some habitat patches are vacant because of the higher risk of "disappearance" of spawners in small habitats and the lower rate of colonization of isolated habitats (Hanski, 1996). For management purposes herring in British Columbia have been divided into five major migratory stocks, and a number of minor stocks which spawn outside the five main stock assessment areas (Schweigert 2003). Tag returns (Hay et al 2001) and DNA microsatellite analyses (Beacham et al 2001) indicate there is significant dispersal (straying) between the major stocks, and there are no significant genetic differences between them. These five major stocks form the bulk of the metapopulation (Ware and Schweigert 2002). Genetic analyses to clarify how closely the minor stocks are linked to the metapopulation are currently in progress. In this paper we examine the dynamic utilization of the available spawn habitat by herring in BC over the last 60 years, by analyzing the occurrence of spawn "disappearance" and "recolonization" events.

Methods

Spawn Time Series and Variables. The British Columbia coastline has been partitioned into 108 areas, called "sections" (Figs 1-3), where herring have spawned at some time either recently, or in the past (Hay and Kronlund 1987, Haist and Rosenfeld 1988). On average, a section contains about 250 km of coastline. However, some sections have considerably longer or shorter coastlines than others.

The length, width and layers of herring spawn deposited along the BC coast have been measured since 1928. However, prior to 1943 the records are incomplete because many areas were not surveyed. We use the spawn habitat index (SHI) developed by Hay and Kronlund (1987) to describe the relative amount of spawn habitat utilized in each section in each spawning season. The spawn habitat index is defined as the length of spawn x [median (width*layers) of spawn] (*for details see http://www.pac.dfo-mpo.gc.ca/sci/herring/herspawn/pages/project_e.htm#bookmark1*). Because the earliest data in the records are considered to be incomplete, the spawn time series that we use span the period 1943 to 2002 (60 years).

The spawn summary time series compiled by Hay et al (available online at *http://www.pac.dfo-mpo.gc.ca/sci/herring/bulletin.htm*) list the annual total length of spawn, mean width, mean egg layers and the spawn habitat index (SHI) for each section since 1943. We used these data to calculate an average SHI for each section. To remove the possible bias caused by missed surveys, we also calculated the average SHI when the section was occupied by spawners (O-SHI):

$$O\text{-}SHI_i = \sum^N SHI_i / [N\text{-}N_{0,i}]$$

where $\sum^N SHI_i$ is the annual SHI_i summed over the length of the time series (N), and $N_{0,i}$ is the number of zero entries in the time series for section (i). Thus, the value of $0\text{-}SHI_i$ indicates the average amount of spawn habitat utilized by herring when they spawn in section (i). We also calculated the average length (km) of spawn in each section when it was occupied ($O\text{-}Length_i$):

$$O\text{-}Length_i = \sum^N Length_i / [N\text{-}N_{0,i}]$$

where $\sum^N Length_i$ is the annual length of spawn summed over the length of the time series (N), and $N_{0,i}$ is the number of zero entries in the time series for section (i). The total length of spawn measured along the BC coast annually is an index of spawner abundance, as it is highly correlated ($r = 0.78$, $P < 0.0001$) with age-structured model estimates of total spawner biomass (Schweigert 2003).

BC Herring Stock Structure. Herring populations in British Columbia have been divided into five major, migratory spawning stocks: Prince Rupert District (PRD), Queen Charlotte Islands (QCI), Central Coast (CC), Georgia Strait (GS) and the West Coast of Vancouver Island (WCVI) (Schweigert 2003). A number of sections are also occupied by minor herring stocks, which spawn outside the five major stock assessment areas in some Regions. The sections occupied by Major and Minor herring stocks in each Region are summarized in the following table:

Region	Major Stock Sections	Minor Stock Sections
PRD	31,32,33,41,42,43,52,51,53	None
QCI	6, 23,24,21,25	1,2,3,4,5,11,12,22
CC	67,71,72,73,74,75,76,77,78,85	61,62,63,64,65,66,81,82,83,84,86,91,92,93, 101,102,103
JS	None (Sections 132 and 135 are included in the Georgia Strait stock assessment area)	111,112,121,122,123,124,125,126, 127,131,133,134,136
GS	132,135,141,142,143,151,152,161, 162,163,164,165,171,172,173,181, 182,191,192,193, 280,291,292,293	201,202
WCVI	231,232,233,241,242,243,244,245, 251, 252,253	220,211,261,262,263,271,272,273,274

For some statistical tests there were not enough data to do a Regional analysis. In these cases the data were pooled into a Northern area, which includes all the sections in the PRD, QCI and CC Regions, and a Southern area, which includes all the sections in Johnstone Strait (JS), GS and WCVI.

Spawn Disappearance and Recolonization Events. In BC, herring typically mature at age 2+ and then spawn annually until they die. The maximum lifespan is about 15 years. We assumed that a *"Disappearance Event"* (DE) occurred in a section when five consecutive years of "no spawn" appeared in the time series. For example, consider the following time series of coded spawn data: ...1100000..., where 1 indicates that spawning occurred in year t, and 0= no spawning in year t. We choose five consecutive years of zeros because this implies that no age 2+, 3+ or 4+ progeny arising from the last recorded spawning in the section could have returned to spawn. In fact, it is quite probable that a four year run of zeros represents a disappearance event. However, we choose the more stringent "five year run of zeros" definition to minimize overestimating the number of spawn disappearance events. To calculate the duration of a disappearance event and the proportion of zeros in the time series, runs of "zeros" at the beginning of the records (in 1943) were not included. Instead, we assumed that the section had not been surveyed, and that the time series began with the first recorded spawn.

Failure to survey a section will influence our results, because we are analyzing the spawn data with respect to "occupied" (spawn present in year t) or "vacant" (no spawn in year t). Therefore, "zero" entries in the time series pose a problem, because we don't always know if "0" means: 1) that the section wasn't surveyed (so some spawns may have been missed), or 2) that it was surveyed and no spawns were observed. Because we require at least five consecutive "zero" records to declare a "Disappearance Event", the amount of bias caused by missing surveys in sections with medium to large SHI indices should be very small. On the other hand, it is possible that some sections with very small SHI_i indices may not have been surveyed for five consecutive years. Therefore, our estimate of the frequency of disappearance events in sections with the smallest O-SHI_i values could be overestimated.

A *"Recolonization Event (RCE)"* was assumed to have occurred when spawning was recorded after a disappearance event. The recolonization pattern was described by a numeric code, where each number in the code represents a year in the spawn time series for a particular section. The following numbers appear in the code: 0= no spawning, 1= spawning occurred. For example, ...00000/111000..., indicates that the section was vacant for five years before a recolonization event occurred (this is defined as year 1 of the RC event). In this example, spawning also occurred in years 2 and 3, but not in year 4, 5 or 6 of the recolonization. This recolonization pattern is classified as unsuccessful because no *potential* progeny of the original colonizers returned to spawn in years 4, 5 or 6 of the event. Other types of unsuccessful recolonization patterns are summarized in Table 1. All other numerical patterns were classified as successful recolonizations.

Table 1. Unsuccessful recolonization patterns found in the spawn timeseries. Because five years of data are required to determine whether or not a recolonization event was successful, some recolonization events at the end of the spawn records in a number of sections cannot be classified yet. Consequently, the number of classified recolonization events is less than the total number of events in the spawn records.

Recolonization pattern	Description
10000... 110000... 1110000... 1010000...	Unsuccessful recolonizations. No age 2+ or 3+ progeny from year 1, 2 or 3 spawners returned to spawn.

Spawn Data. We analyzed the spawn time series for 76 of the 108 herring sections shown in Figs 1-3. Seven sections were excluded because there was no recorded spawn in the time series. Another seven sections were excluded because they did not experience at least one successful recolonization event between 1943 and 2002. This indicates that the spawn habitat in these 14 sections was utilized erratically by herring. After consultations with people who are familiar with the spawn data (L. Hamer and D. Hay, DFO. personal communication), we excluded another 18 sections because they were either very small, or very remote from the main spawning areas and therefore may not have been surveyed regularly (Table 2). By excluding these 18 sections, we are intentionally deriving a more conservative estimate of the frequency of herring *Disappearance* and *Recolonization* events along the coast. The 32 sections that were excluded for the reasons outlined above contained less than 1% of the spawn habitat (SHI). Accordingly, the 76 sections we analyzed represent virtually all the herring spawn habitat in BC.

Table 2. Total number of sections in each Region. The number of sections included in our analysis, and the number of sections excluded by Region [listed in square brackets] for the reasons outlined above.

Region	# Sections	# Analyzed	# Excluded
Prince Rupert District (PRD)	9	6	3 [31,32, 41]
Queen Charlotte Islands (QCI)	13	7	6 [1,2,3,4,5,11]
Central Coast (CC)	27	19	8 [61,63,64,65,71,81,91, 101]
Johnstone Strait (JS)	13	10	3 [111,121,131]
Georgia Strait (GS)	26	18	8 [151,161,171,192, 291,292,201,202]
West Coast Vancouver Island (WCVI)	20	16	4 [211,220,261,271]
Total	**108**	**76**	**32**

Results

Examples of Disappearance and Recolonization Events. In some cases, disappearance and successful recolonization sequences evolved in four phases: 1) a period of spawn decline; 2) a period where the spawn was very low and fluctuated erratically; 3) five (or more) consecutive years of no spawn – the disappearance event; and 4) a recolonization event that began with the appearance of a small amount of spawn, followed by an increase in spawn length over time.

For example, the Nanoose Bay (Section 172) record contains a four-phase sequence (Fig.4). This section is part of the main spawning area in Georgia Strait and has a large amount of potential spawn habitat (O-SHI index = 574,500). Accordingly, it is closely monitored every year; so a spawn would have been surveyed if it occurred. In other words it is virtually certain that a run of four or more zeros in this section indicates that there was no spawning, and that a disappearance event occurred. Fig. 4 shows that the spawn in Nanoose Bay declined from 1974 to 1984 (Phase 1), and then fluctuated erratically for the next three years (Phase 2), before it finally disappeared in 1988. For the next four years (1988 to 1991), herring did not spawn in Nanoose Bay (Phase 3). We recall that this event was noticed at the time by local herring managers and fishermen and was considered to be mc ' "unusual". A small amount of spawn reappeared in 1992, and then steadily increased for the next seven years (Phase 4). Although this example fails to meet our stringent definition of a disappearance event (we require 5 consecutive years without spawn), it probably was, because of the way in which the spawn declined, disappeared, and then reappeared. Another example of a four phase disappearance and recolonization sequence occurred in N. Porcher Island (Section 43, Fig. 4) between 1945 and 1985. In this case, the disappearance event lasted 6 years (1963 to 1968) before the section was successfully recolonized in 1969.

The Hesquiat Harbor (Section 242) spawn time series contains a three phase disappearance and recolonization sequence (Phases 1, 3 and 4; Fig. 5). In this case, note how slowly the average spawn length increased during the recolonization phase. To highlight how variable the amount of spawn can be from one year to the next at these small spatial-scales, note that 8-km of spawn was recorded in Hesquiat Harbor in 2000, while no spawning occurred in 2001 and 2002.

A striking example of a section that was vacant for a very long time (28 years) before it was successfully recolonized (in 1980), occurred in Mathieson and Spiller Channels (Section 78, Fig. 5). This was the longest disappearance event in the records that we examined, which finally ended with a successful recolonization.

There are also examples which suggest the well-documented climate regime change in BC in 1976/77 (e.g. Ware 1995) may have caused, or at least have been a factor involved in some very long disappearance events (> 19 years). For instance, in Clannick Cove on the WCVI (Section 262) a DE occurred abruptly in 1978 (Fig. 6). The area remained vacant for the next 20 years. A small amount of spawn reappeared at the end of the warm regime in 1998, and increased significantly during the cooler period that prevailed between 1999 to 2002. Another example of a possible DE associated with the recent warm regime occurred in Plumper Sound (Section 182). Here, the spawn declined abruptly when the warm regime began, and then disappeared a few years later (Fig. 6). However, unlike Clannick Cove, Plumper Sound has not been recolonized yet.

Disappearance Events. In the 76 sections we analyzed, 42 sections (55%) experienced one or more disappearance events between 1943-2002 (Fig. 7). Nineteen sections (25%) had 1 disappearance event; 12 sections had 2 disappearances, 6 sections had 3 disappearances, 4 sections had 4 disappearances, and 1 section had 5 disappearances. In contrast, the remaining 34 sections (45%) had continuous spawning records (i.e. no gaps longer than 4 years; see Appendix Table A3 for a list of these sections). Table 3 shows that the percentage of sections experiencing disappearance events was similar in each region.

Table 3. Number of sections in each Region with disappearance events.

Region	Sections Analyzed	Sections with Disappearances	Section Number
PRD	6	3 (50%)	43,51,53
QCI	7	3 (43%)	12,22,23
CC	19	11 (58%)	62,66,73,75,78,82, 83,84,86,92,103
JS	10	5 (50%)	112,123,124,133,136
GS	18	12 (67%)	135,141,152,162, 163,164,165,182, 191,193,280,293
WCVI	16	8 (50%)	231,233,241,242, 251,262,263,274
Total	**76**	**42 (55%)**	

For the rest of this paper, the results are presented in the form of a series of questions and answers. We hope this will make it easier for a reader to find a particular topic of interest.

Do disappearance events occur more frequently in more remote sections? Intuitively, one would expect that more remote sections are likely to be sampled less frequently (i.e. more missing surveys, and therefore more zero entries). We examined this possibility by indexing the remoteness of each section from the main spawning area in each region. A remoteness index = 1 indicates that the section is in the main spawning area. A remoteness index = 2 indicates that the section is along (or directly adjacent) to the outer coast, but is a moderate distance from the main spawning area. A remoteness index = 3 indicates that the section is far away from the main spawning area. This category includes sections that occupy the midsections and heads of the long coastal inlets (Figs. 1-3).

The data do not support the idea that the more remote (Category 3) sections have more disappearance (and less recolonization) events than the less remote (Category 2) sections. An ANOVA (and Tukey HSD multiple comparison test) indicates that the slightly higher average number of disappearance events ($p=0.94$) and frequency of zeros in the spawn records ($p=0.63$) of Category 3 sections are not significantly different from the less remote Category 2 sections (Fig. 8, Table 4). Therefore, Category 3 sections are as likely to be surveyed as Category 2 sections. In contrast, Category 1 sections have significantly more spawn habitat ($p<0.02$), a significantly lower frequency of zeros ($p<0.01$), and significantly lower average number of disappearance events ($p<0.01$) than Category 2 and 3 sections (Fig.8; Table 4). This indicates that Category 1 sections, which occur in the main spawning areas in each Region contain more spawn habitat (mean O-SHI), on average, and therefore are more consistently occupied by herring. In contrast, sections outside the main spawning area, tend to contain smaller amounts of spawn habitat, on average, and therefore are more likely to experience disappearance events.

Table 4. Number of sections, the average amount of occupied spawn habitat, the average frequency of zeros, and the average number of disappearance (DE) and recolonization (RCE) events per section in the 60-yr time series, in each remoteness category.

Category	# Sections	Mean O-SHI	Frequency of zeros	Mean DE	Mean RCE
1	32	347.8	6.9	0.03	0.03
2	32	98.7	26.9	1.81	1.41
3	12	36.2	30.2	1.92	1.50

Are there differences in the average number of disappearance and recolonization events between Regions and between Major and Minor stock Sections?

To examine this question, we sorted the Major and Minor herring stock sections into their respective Regions, for an ANOVA. Significant differences in five variables were found between the Central Coast Major and Minor stock sections (Table 5). The Minor stock sections in this Region had significantly less spawn habitat *(p=0.03)*, and significantly more Disappearance *(p=0.03)* and Recolonization *(p=0.05)* events on average than the Major stock sections. A similar comparison of the Georgia Strait Major stock sections with the Johnstone Strait Minor stock sections indicated that the Minor stock sections had significantly less spawn habitat *(p=0.03)*, but that there were no significant differences in the average number of Disappearance and Recolonization events. On a coastwide basis, Minor stock sections contain significantly less *(p=0.002)* spawn habitat (64.9 thousand units) than Major stock sections (264.7 thousand units), but the average number of Disappearance and Recolonization events was only significantly different in the Central Coast.

A Regional comparison of the Major stock sections indicated that there were no significant differences in the six variables shown in Table 5. A Regional analysis of the Minor stock sections revealed only one significant difference: the minor stocks in Johnstone Strait have a significantly lower mean number of recolonizations (0.30 per section in 60-yrs) than the Central Coast minor stock sections (1.80 per section in 60-yrs; $p = 0.03$).

Table 5. Mean number of disappearance events (DE) and recolonization events (RCE), frequency of zeros, spawn habitat index (SHI, thousands of units), occupied-SHI (O-SHI, thousands of units), and occupied spawn length (O-length, km) for the Major and Minor stock sections during the 60-yr time series. Shaded differences in the means between Major and Minor stock sections in the same Region are significant ($p < 0.05$).

Region-Stock	# of sections	Mean DEvents	Mean RCEvents	Mean Freq.Zeros	Mean SHI (thousands)	Mean O-SHI (thousands)	Mean O-length (km)
QCI-Major	5	0.40	0.20	12.2	183.7	220.1	8.07
QCI-Minor	2	1.50	0.50	19.1	49.6	110.2	5.50
PRD-Major	6	1.50	1.50	17.2	297.0	319.8	7.40
PRD-Minor	0						
CC-Major	9	0.56	0.56	12.3	127.4	146.9	11.35
CC-Minor	10	2.00	1.80	26.3	30.58	56.4	7.46
JS-Major	0						
JS-Minor	10	0.70	0.30	15.8	32.9	40.5	6.41
GS-Major	18	1.17	0.94	21.2	313.8	384.1	6.75
GS-Minor	0						
WCVI-Major	11	1.00	0.73	18.9	140.3	155.9	4.56
WCVI-Minor	5	0.80	0.40	23.8	89.6	122.5	2.81
Coastwide-Major	49	0.98	0.82	17.6	225.3	264.7	7.31
Coastwide-Minor	27	1.26	0.89	21.4	43.8	64.9	6.06
Coastwide-All	76	1.08	0.84	19.0	160.8	193.7	6.87

Are there differences in the average number of disappearance and recolonization events between Regions and between Major and Minor stock Sections?

To examine this question, we sorted the Major and Minor herring stock sections into their respective Regions, for an ANOVA. Significant differences in five variables were found between the Central Coast Major and Minor stock sections (Table 5). The Minor stock sections in this Region had significantly less spawn habitat *(p=0.03)*, and significantly more Disappearance *(p=0.03)* and Recolonization *(p=0.05)* events on average than the Major stock sections. A similar comparison of the Georgia Strait Major stock sections with the Johnstone Strait Minor stock sections indicated that the Minor stock sections had significantly less spawn habitat *(p=0.03)*, but that there were no significant differences in the average number of Disappearance and Recolonization events. On a coastwide basis, Minor stock sections contain significantly less *(p=0.002)* spawn habitat (64.9 thousand units) than Major stock sections (264.7 thousand units), but the average number of Disappearance and Recolonization events was only significantly different in the Central Coast.

A Regional comparison of the Major stock sections indicated that there were no significant differences in the six variables shown in Table 5. A Regional analysis of the Minor stock sections revealed only one significant difference: the minor stocks in Johnstone Strait have a significantly lower mean number of recolonizations (0.30 per section in 60-yrs) than the Central Coast minor stock sections (1.80 per section in 60-yrs; *p = 0.03*).

Table 5. Mean number of disappearance events (DE) and recolonization events (RCE), frequency of zeros, spawn habitat index (SHI, thousands of units), occupied-SHI (O-SHI, thousands of units), and occupied spawn length (O-length, km) for the Major and Minor stock sections during the 60-yr time series. Shaded differences in the means between Major and Minor stock sections in the same Region are significant ($p < 0.05$).

Region-Stock	# of sections	Mean DEvents	Mean RCEvents	Mean Freq Zeros	Mean SHI (thousands)	Mean O-SHI (thousands)	Mean O-length (km)
QCI-Major	5	0.40	0.20	12.2	183.7	220.1	8.07
QCI-Minor	2	1.50	0.50	19.1	49.6	110.2	5.50
PRD-Major	6	1.50	1.50	17.2	297.0	319.8	7.40
PRD-Minor	0						
CC-Major	9	0.56	0.56	12.3	127.4	146.9	11.35
CC-Minor	10	2.00	1.80	26.3	30.58	56.4	7.46
JS-Major	0						
JS-Minor	10	0.70	0.30	15.8	32.9	40.5	6.41
GS-Major	18	1.17	0.94	21.2	313.8	384.1	6.75
GS-Minor	0						
WCVI-Major	11	1.00	0.73	18.9	140.3	155.9	4.56
WCVI-Minor	5	0.80	0.40	23.8	89.6	122.5	2.81
Coastwide-Major	49	0.98	0.82	17.6	225.3	264.7	7.31
Coastwide-Minor	27	1.26	0.89	21.4	43.8	64.9	6.06
Coastwide-All	76	1.08	0.84	19.0	160.8	193.7	6.87

Is there a relationship between the average spawn habitat index and the disappearance event probability? To address this question, the 76 sections were divided into four categories based on their average O-SHI (Fig. 9). Coastwide, the conditional probability of one or more disappearance events in the 60-yr spawn time series was very high (0.88) for sections with the smallest average spawn habitat index (O-SHI < 47 thousand units). For sections with average spawn habitat indices (47 to 147 thousand units), the probability was lower (0.48). For sections with large spawn habitat indices (148 to 500 thousand units) the probability of a disappearance event was 0.38. No DE's occurred in the seven largest sections, which each contained more than 500 thousand O-SHI units (Table 6). There were not enough sections in QCI and PRD to also do this analysis by Region, so we repeated it for the Northern sections (PRD,QCI and CC) and the Southern sections (JS,GS and WCVI) to see if there were any obvious North-South differences (Table 6). The results indicate that except for a few minor differences, the conditional disappearance probabilities in the North and the South are similar for sections with comparable amounts of spawn habitat (Fig. 10).

Table 6. Coastwide and North-South conditional disappearance probabilities were estimated by dividing the number of sections with one or more disappearance events, by the total number of sections in each O-SHI group. DE = disappearance event, RCE = recolonization event.

O-SHI range (thousands)	Number of Sections	Average O-SHI in Group (thousands)	Probability of one or more DE	Average number of DE per section in 60-yrs	Average number of RCE per section in 60-yrs
Coastwide					
< 47	26	26.2	0.88	1.77	1.31
47-147	26	87.0	0.48	0.93	0.78
148-500	17	284.2	0.38	0.69	0.56
> 500	7	> 500	0.00	0.00	0.00
Northern Sections					
< 47	8	30.6	1.00	2.37	2.25
47-147	12	92.6	0.50	1.17	0.92
148-500	10	229.6	0.30	0.60	0.50
> 500	2	> 500	0.00	0.00	0.00
Southern Sections					
< 47	18	25.4	0.84	1.63	1.05
47-147	14	85.2	0.43	0.50	0.43
148-500	7	335.8	0.57	0.86	0.71
> 500	5	> 500	0.00	0.00	0.00

What is the average duration of a disappearance event? Coastwide, we found 82 disappearance events in the spawn time series. Including data from the sections that are currently vacant, disappearance events last an average of 11.0 years, (median = 8.0 yrs; minimum = 5 yrs; maximum = 35 yrs;).

We also examined the data by Region to determine if there were any significant differences in the average duration of disappearance events. The data summarized in Table 7 show that the Regional medians and means tend to cluster into two groups: Group 1 = PRD, CC, and JS, and Group 2 = GS, WVCI and QCI. An ANOVA confirmed that disappearance events have lasted significantly longer, on average ($p=0.0025$), in the Group 2 Regions. The DE duration conditional probability distributions for each group are shown in Fig. 11.

Table 7. Number of disappearance events, the average duration (yrs) and median values by Region. The Group 2 Regions are shaded.

Region	Number of DE Events	Average DE duration (yrs)	Median DE duration (yrs)
PRD	9	7.8	6.0
QCI	5	13.8	14.0
CC	25	8.6	7.0
JS	8	10.9	6.5
GS	20	12.2	9.5
WCVI	15	14.6	12.0

Six sections had disappearance events lasting longer than 19 years that finally ended with a successful recolonization (Table 8). The longest DE in the records, which was successfully recolonized occurred in section 78 (Mathieson and Spiller Channels). It lasted 28 years (Fig. 5).

Table 8. Longest disappearance events that ended with a successful recolonization.

Section	Longest DE (yrs) that ended with a successful recolonization	Period Section wasVacant
23	23	1944-1967
78	28	1952-1980
141	23	1960-1983
162	22	1978-2000
191	20	1973-1993
262	20	1978-1998

Eighteen sections are currently vacant (Table 9), and have been vacant for an average of 15.7 yrs (median = 14 yrs; minimum = 5 yrs; maximum = 35 yrs). It is significant that thirteen (72%) of the eighteen vacant sections occur in Southern BC.

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Table 9. Locations of "Vacant" sections in 2002.

Region	Sections Analyzed	Sections currently Vacant	Vacant Major Stock Sections	Vacant Minor Stock Sections
PRD	6	0 (0%)		
QCI	7	3 (43%)	23	12,22
CC	19	2 (10%)		62, 84
JS	10	4 (40%)		112,123,124,136
GS	18	4 (22%)	164,182,193, 293	
WCVI	16	5 (31%)	231,241,251,	263, 274
Total	76	18 (24%)	8	10

An ANOVA indicated that the vacant sections listed in Table 9 have a smaller average spawning habitat (O-SHI), experience significantly more disappearance events, and therefore have a significantly higher frequency of zeros in the spawn time series than currently occupied sections (Table 10).

Table 10. ANOVA and Tukey test results comparing the average characteristics of sections that were "Vacant" in 2002, with the "Occupied" sections.

Variable	Currently Vacant mean	Currently Occupied mean	*p*
Occupied-SHI	60.2	235.2	*0.07*
Mean number of DEs in 60-yr time series	1.89	0.83	*<0.001*
Mean number of zeros in 60-yr time series	30.2	15.5	*<0.001*

Are there periods in the spawn record where Disappearance Events occur and end more frequently? The disappearance and recolonization rate time series (number of sections/year) in the Southern and Northern Regions are shown in Figs 12 and 13. In the South, the disappearance rate increased rather abruptly in 1979. The tendency toward a higher recolonization rate is also apparent in the latter part of that time series (Fig. 12). Two well-documented changes occurred since 1943 that may have affected the spawn disappearance and recolonization rates: 1) a protracted warm climate regime began in BC in 1977; and 2) scuba spawn surveys began to steadily replace surface surveys along the BC coast after 1986 (Hay and McCarter 1999, Schweigert 2003).

A series of ANOVA and Tukey comparison tests were made to determine if there were any significant differences in the mean disappearance and recolonization rates after the 1977 climate regime change, or with the change in spawn survey methods. For the first test, the data were divided into two periods: 1) before the warm regime began (1943-76); and 2) during the warm regime (1977-1998). The following table shows that the mean disappearance and recolonization rates were higher during the warm regime in both the Southern and Northern Regions. However, the disappearance rate was only significantly higher in the South ($p=0.02$).

Table 11. Mean disappearance (DE) and recolonization (RCE) rates in the Southern and Northern sections during two different climate regimes.

Period	Mean Disappearance rate and (SD) (Sections/yr)	Mean Recolonization rate and (SD) (Sections/yr)	DE-RCE rates (Sections/yr)
South			
1=1943-1976	0.55 (0.67)	0.41 (0.75)	+ 0.14
2=1977-1998	1.14 (1.08)	0.68 (0.89)	+ 0.46
p	*0.02*	*0.25*	
North			
1=1943-1976	0.58 (0.19)	0.59 (0.75)	- 0.01
2=1977-1998	0.91 (1.02)	0.64 (0.79)	+ 0.27
p	*0.16*	*0.84*	

The difference between the mean disappearance and recolonization rates (DE-RCE) increased in the North, and particularly in the South after 1976. This means that spawn was disappearing faster in some sections during the warm regime than it was reappearing through recolonization. In fact, the spawn records suggest that the warm regime may have had a negative impact on at least eleven sections in southern BC: Section 123, 162, 164, 165, 181, 182, 252, 262, 263, 274, and 293 (see Appendix Table A1).

For the second test, the data were divided into two periods corresponding to the change in spawn survey methods: 1) surface survey period 1943-1986; 2) scuba survey era 1987-2002. The following table shows that the mean disappearance and recolonization rates were higher after 1986. In this case, the increase in the disappearance rate was significant in the North, but not in the South. On the other hand, the recolonization rate was significantly higher in the South after 1986, but not in the North.

Table 12. Mean disappearance (DE) and recolonization (RCE) rates in the Southern and Northern sections during the surface survey period (1) and the scuba survey era (2).

Period	Mean Disappearance rate and (SD) (Sections/yr)	Mean Recolonization rate and (SD) (Sections/yr)
South		
1=1943-1986	0.72 (0.80)	0.38 (0.68)
2=1987-2002	1.00 (1.21)	1.07 (1.10)
p	*0.34*	*0.008*
North		
1=1943-1986	0.58 (0.76)	0.57 (0.73)
2=1987-2002	1.17 (1.03)	0.81 (0.91)
p	*0.034*	*0.30*

Table 9. Locations of "Vacant" sections in 2002.

Region	Sections Analyzed	Sections currently Vacant	Vacant Major Stock Sections	Vacant Minor Stock Sections
PRD	6	0 (0%)		
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p	*0.02*	*0.25*	
North			
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2=1977-1998	0.91 (1.02)	0.64 (0.79)	+ 0.27
p	*0.16*	*0.84*	

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1=1943-1986	0.58 (0.76)	0.57 (0.73)
2=1987-2002	1.17 (1.03)	0.81 (0.91)
p	*0.034*	*0.30*

Of course, the previous two tests are confounded by the fact that it was warm during most of the scuba survey era, and cool during most of the surface survey era. Accordingly, for the third test, the data were divided into three periods: 1) before the warm regime (and scuba surveys) began (1943-76); 2) the first half of the warm regime, before the scuba surveys began (1977-86); and 3) the latter half of the warm regime, when scuba surveys began to replace surface surveys (1987-2002). The ANOVA results are shown in Table 13.

Table 13. Mean disappearance and recolonization rates in the South and North during different periods. The last column shows the net rate of change (difference between the disappearance rate and the recolonization rate). A positive difference indicates that the disappearance rate was higher than the recolonization rate.

Period	Mean Disappearance rate and (SD) (Sections/yr)	Mean Recolonization rate and (SD) (Sections/yr)	DE-RCE (Sections/yr)
South			
1=1943-1976	0.55 (0.67)	0.41 (0.75)	+ 0.14
2=1977-1986	1.30 (0.95)	0.30 (0.48)	+ 1.00
3=1987-2002	1.00 (1.21)	1.07 (1.10)	- 0.07
	p (1,2) = 0.047	*p (1,3) = 0.044* *p (2,3) = 0.070*	
North			
1=1943-1976	0.57 (0.71)	0.59 (0.75)	- 0.02
2=1977-1986	0.60 (0.97)	0.50 (0.71)	+ 0.10
3=1987-2002	1.17 (1.03)	0.81 (0.91)	+ 0.36
	p (1,3) = 0.099		

In the South, Table 13 shows that the mean disappearance rate increased by 0.75 sections/yr during the first part of the warm regime (Period=2; *p=0.047*). In contrast, the mean recolonization rate didn't increase until the last half of the warm regime (Period 3), when it became significantly higher than it was during Period 1 (*p=0.044*), and probably Period 2 (*p=0.07*). During the cool regime (1943 to 1976) the average disappearance and recolonization rates were similar (in balance on average). This means that spawn was reappearing in some sections at about the same rate that it was disappearing in others. However, this balance shifted during the first half of the warm regime (Period 2), when the mean disappearance rate increased and was more than four times as large as the recolonization rate. Consequently, in the South during the first half of the warm regime there was a net decrease in the number of sections containing spawn. However, by the end of the warm regime, the mean disappearance and recolonization rates, although higher, were once again more balanced (Fig. 14).

Of course, the previous two tests are confounded by the fact that it was warm during most of the scuba survey era, and cool during most of the surface survey era. Accordingly, for the third test, the data were divided into three periods: 1) before the warm regime (and scuba surveys) began (1943-76); 2) the first half of the warm regime, before the scuba surveys began (1977-86); and 3) the latter half of the warm regime, when scuba surveys began to replace surface surveys (1987-2002). The ANOVA results are shown in Table 13.

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3=1987-2002	1.00 (1.21)	1.07 (1.10)	- 0.07
	p (1,2) = 0.047	*p (1,3) = 0.044* *p (2,3) = 0.070*	
North			
1=1943-1976	0.57 (0.71)	0.59 (0.75)	- 0.02
2=1977-1986	0.60 (0.97)	0.50 (0.71)	+ 0.10
3=1987-2002	1.17 (1.03)	0.81 (0.91)	+ 0.36
	p (1,3) = 0.099		

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In the Northern sections, although the differences in the mean disappearance and recolonization rates between the three periods are not significant (Table 11), over the length of the time series, the DE rates in the North and South are positively correlated (*p=0.009*). This means that when the DE rate was higher in the North, it also tended to be higher in the South. The Northern and Southern recolonization rate time series are also positively correlated (*p=0.015*).

What proportion of Recolonization Events are successful? Recolonization events were classified into two types: successful or unsuccessful (see Methods). Only 53% of the attempted recolonization events were successful.

How does the spawn length change during a successful recolonization? A logistic equation (Ricklefs 1990) was used to describe the observed changes in spawn length during a recolonization event:

$$Y_{i,t} = K_i / (1 + B_i * EXP[- r_i * t]) \quad (1)$$

Here, $Y_{i,t}$ is the kilometers of spawn in section *i* in year *t*; K_i is the equilibrium spawn length under current conditions in section *i*; B_i is the scaled size of the spawn length at time zero; and r_i is the maximum exponential rate of increase.

We estimated the parameters (K_i, B_i and r_i) in equation 1 from the measured length of spawn in specific sections. At the "section" spatial-scale, the length of spawn (L, km) is highly correlated with the spawn habitat index (SHI). We also estimated the recovery time, which is the number of years required for the spawn length to reach "equilibrium". An interesting example of a very slow recovery occurred in Hesquiat Harbor, where the spawn length increased for 42-yrs (between 1958-2000; Fig. 15). In contrast, the spawn length in Baynes Sound reached "equilibrium" in only ten years (Fig. 15). In both of these examples, the general increase in spawn length clearly fits the logistic model. However, at this small spatial-scale Figs. 4, 5, 6 and 15 clearly show that there is also a lot of interannual variability, presumably due to large variations in straying by herring between nearby sections, from one spawning season to the next.

The parameters in equation 1 were estimated for each section using the non-linear curve-fitting program in SYSTAT. For this analysis, the sections were divided into two groups: 1) Group 1 contained the sections with no disappearance events in the spawn time series; and 2) Group 2 contained the sections, which experienced one or multiple disappearance events. For Group 1 the logistic parameters were estimated during the mid-1960s to 1980s period (see Appendix Table A2). During the mid-1960s an intense reduction fishery depleted the biomass of herring along the BC coast. The spawner biomass began to recover in the late-1960s and 1970s in response to the closure of the fishery (1968-71) and the lower harvest rates that followed when the "new" roe

fishery reopened in the early 1970s. For the Group 2 sections, the logistic parameters were estimated during specific recolonizing events (see Appendix Table A2). The results are presented in Table 12. The recovery times for the Group 1 spawning aggregations ranged from 1 to 15-yrs, and 2 to 40 for the Group 2 aggregations. On average, at the section spatial-scale herring spawning aggregations require about 7 to 10 years to recover from a low abundance level. The recovery times were not significantly different between the Group 1 and 2 sections. However, there is an indication that the average, maximum exponential rate of increase in spawn is higher in Group 1 sections ($p=0.04$), possibly because these sections may contain higher quality spawn habitat.

Table 14. T-tests comparing the mean growth parameters and recovery times in Group 1 and Group 2 sections. For both groups, the recovery time indicates the number of years the length of spawn required to reach "equilibrium" (see Appendix Table A2).

Variable	Group 1 mean	Group 2 mean	*p*
Equilibrium "abundance" (K, kms of spawn)	14.98	11.36	*0.19*
Maximum rate of increase [r]	1.22	0.55	*0.04*
Recovery time (yrs)	7.41	10.55	*0.17*

On average, how long do successful recolonizations last? This is a difficult question to answer because many sections that were recolonized sometime in the past have been continuously utilized by herring for the 60-yr length of the spawn time series. Perhaps the best way to address this question is to note that so far the longest successful recolonization took about 42-yrs (Section 242, Hesquiat Harbor) to complete, while the shortest took only 4-yrs. Three sections have a history of short recolonizations: Section 51 had two successful recolonizations, each of which lasted only four years; Section 53 had two successful recolonizations lasting 8 and 11-yrs respectively; and Section 193 had two successful recolonizations lasting just 4 and 6-yrs respectively. In these three sections it appears that the spawn habitat is probably marginal because herring don't occupy these habitats for very long before the next disappearance event occurs.

Do more recolonizations occur when the abundance of spawners in the metapopulation is high? We examined this question by calculating the correlation coefficient between the coastwide number of recolonization events that occurred in year *t* and the abundance of spawners in the same year measured as: 1) the total length of spawn, and 2) the total biomass of spawners estimated by the 2003 age-structured model (Schweigert 2003). The results were equivocal. There was no correlation between the frequency of recolonization events during climate Period 1 (1943-1976) and either the coastwide total length of spawn, or the spawner biomass. However, during the warm climate regime (1977-98) there was a positive correlation between the frequency of recolonization events and spawn length ($p=0.059$). However, the correlation was

much weaker with the spawner biomass ($p=0.50$). These ambiguous findings suggest that during the warm regime, there was a very weak tendency for recolonizations to occur more frequently when the abundance of spawners in the metapopulation was high. Apparently other factors are more important.

What is Regional pattern in the biomass of the Metapopulation? To answer this question, we ran a principal component analysis (SYSTAT) using the estimated spawner biomass time series (1951-2003) for the five major stocks from (Schweigert 2003). The objective of a Principal Components analysis is to take p variables, in this case the spawner biomass time series for the five major stocks, and find combinations of these variables, which produce indices (principal components) that are uncorrelated with each other. The lack of correlation is a useful property because it means that these indices are measuring different "dimensions" in the data. The first principal component accounts for the largest amount of variation in the data, while the second principal component accounts for the second largest amount of variation, and so on. In the spawner biomass data, the first two principal components explained 65% of the total variance. Since all five populations are positively correlated with the first principal component (Factor 1), this component defines the common, regional pattern in the metapopulation (Table 12). As anticipated, Factor 1 is very highly correlated with the coastwide biomass of spawners (Fig. 16).

In contrast, we found that Factor 2 was significantly correlated with the average sea surface temperature along the BC coast (Fig. 17). Table 13 indicates that the major stocks respond differently to Factor 2. In this case, the WCVI and QCI stocks were negatively correlated with Factor 2, while the remaining stocks were positively correlated. This pattern is broadly consistent with previous work which found that recruitment was significantly lower in the WCVI and QCI populations during warm climate regimes (Ware and Schweigert 2002).

Table 15. Correlation matrix component loadings. These are the correlations of the original variables (the stock biomass time series) with the principal components (or factors).

Stock	Factor 1	Factor 2
WCVI	0.616	- 0.582
GS	0.546	0.721
CC	0.832	0.374
QCI	0.714	- 0.539
PRD	0.304	0.128
Variance Explained	39%	26 %

fishery reopened in the early 1970s. For the Group 2 sections, the logistic parameters were estimated during specific recolonizing events (see Appendix Table A2). The results are presented in Table 12. The recovery times for the Group 1 spawning aggregations ranged from 1 to 15-yrs, and 2 to 40 for the Group 2 aggregations. On average, at the section spatial-scale herring spawning aggregations require about 7 to 10 years to recover from a low abundance level. The recovery times were not significantly different between the Group 1 and 2 sections. However, there is an indication that the average, maximum exponential rate of increase in spawn is higher in Group 1 sections ($p=0.04$), possibly because these sections may contain higher quality spawn habitat.

Table 14. T-tests comparing the mean growth parameters and recovery times in Group 1 and Group 2 sections. For both groups, the recovery time indicates the number of years the length of spawn required to reach "equilibrium" (see Appendix Table A2).

Variable	Group 1 mean	Group 2 mean	p
Equilibrium "abundance" (K, kms of spawn)	14.98	11.36	*0.19*
Maximum rate of increase [r]	1.22	0.55	*0.04*
Recovery time (yrs)	7.41	10.55	*0.17*

On average, how long do successful recolonizations last? This is a difficult question to answer because many sections that were recolonized sometime in the past have been continuously utilized by herring for the 60-yr length of the spawn time series. Perhaps the best way to address this question is to note that so far the longest successful recolonization took about 42-yrs (Section 242, Hesquiat Harbor) to complete, while the shortest took only 4-yrs. Three sections have a history of short recolonizations: Section 51 had two successful recolonizations, each of which lasted only four years; Section 53 had two successful recolonizations lasting 8 and 11-yrs respectively; and Section 193 had two successful recolonizations lasting just 4 and 6-yrs respectively. In these three sections it appears that the spawn habitat is probably marginal because herring don't occupy these habitats for very long before the next disappearance event occurs.

Do more recolonizations occur when the abundance of spawners in the metapopulation is high? We examined this question by calculating the correlation coefficient between the coastwide number of recolonization events that occurred in year t and the abundance of spawners in the same year measured as: 1) the total length of spawn, and 2) the total biomass of spawners estimated by the 2003 age-structured model (Schweigert 2003). The results were equivocal. There was no correlation between the frequency of recolonization events during climate Period 1 (1943-1976) and either the coastwide total length of spawn, or the spawner biomass. However, during the warm climate regime (1977-98) there was a positive correlation between the frequency of recolonization events and spawn length ($p=0.059$). However, the correlation was

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Discussion

Some coastal communities in British Columbia believe that each bay where herring spawn contains a genetically discrete stock. Accordingly, if one of these "stocks" fails to return to spawn, the implication is that some unique genetic diversity has probably been lost. Our analysis indicates that sections that have experienced disappearance events cannot contain discrete local populations. The metapopulation concept provides an ecological basis for explaining that small herring spawning aggregations can disappear for a time due to dispersal and other natural causes. And that vacant habitat will be recolonized when suitable conditions return. A key feature of metapopulation thinking is that not all suitable habitats are necessarily occupied simultaneously and, in particular, that some habitat patches are vacant because of the high risk of a disappearance event in especially small patches, and the low rate of colonization of especially isolated patches (Hanski 1996). *We take the definition of homing to mean a return of mature herring to the same spawning area used in the previous year, but not necessarily the one in which the fish lived as an egg, larvae or juvenile* (McQuinn 1997). The tagging data indicate that most mature herring (83%) do not home from one spawning season to the next to the same section (Hay et al 2001). Instead, they stray to other sections to spawn. In fact, Hay et al (1989) noted "frequent occurrences of spawning on 'new' grounds in some years, as well as abandonment of long-used spawning" areas in other years. Hay and Kronlund (1987) also found indications of shifts in spawn among smaller adjacent areas in the Strait of Georgia. We found that the 18 Sections, which are currently vacant, have a smaller amount of spawn habitat, and a higher frequency of disappearance events than the sections containing spawn (Table 10). We also showed that smaller sections have a higher probability of experiencing a disappearance event (Fig. 10), and that vacant habitats are recolonized in less than 11 years on average, presumably by strays from nearby sections. Recolonizations occurred more quickly in the Prince Rupert, Central Coast and Johnstone Strait Regions (median = 7 years) and more slowly in Georgia Strait, West Coast of Vancouver Island, and Queen Charlotte Islands (median=11 years). Some sections were recolonized in less than five years, while at the other extreme Section 136 (Reed Island) has not been recolonized for 35 years, and counting. This section is not particularly remote, which is consistent with our finding that the degree of remoteness from the main spawning area did not have a significant effect on the recolonization rate (Table 4). However, we note that some of the most remote sections in BC were not included in our analysis (see Table 2), so it is possible that these sections could take longer to be recolonized.

In the Southern sections, we found that the balance around unity between the disappearance and recolonization rates changed in the 1970s. During the first half of the warm regime, the disappearance rate increased significantly and was much higher than the recolonization rate (Fig. 14). This means that the number of sections occupied by spawners must have declined in the 1970s and 1980s. Hay and McCarter (1999) noticed this decline. They also observed that there was no change, or a slight increase in the number of locations where herring spawned. They concluded that the observed decline in the number of sections with spawn over the last two decades, but no change, or increases in the numbers of locations with spawn, is consistent with the idea that more herring are concentrating in fewer sections, and spawning at more locations within those sections. We suggest that this phenomenon, in part, may have been caused by "*conspecific attraction*" (Hanski 1996). For example, if environmental conditions change and the quality of the spawning habitat deteriorates in some sections, herring may abandon these poorer quality habitats and be attracted by conspecifics to "better", occupied habitats. Such an "attraction" event may have occurred recently between the WCVI and Georgia Strait. The stock assessment data (Schweigert 2003) indicate that the Georgia Strait and WCVI populations largely fluctuated in-phase from 1951 to about 1989. Since then, the WCVI population declined significantly, while the Georgia Strait population increased (Fig. 18). The results outlined above suggest that conditions in some spawning areas along the WCVI probably declined during the latter half of the warm regime, and that a significant proportion of WCVI herring may have dispersed to Georgia Strait to spawn. Although the tagging data are very spotty, there is some support for this hypothesis: in 1989 and 1990 the straying rate from the WCVI was three times higher (29%) than it had been in earlier years for which there are data (ca. 8%; Ware and Tovey 2000, Table 2B). By analogy, "many species of birds show flexible habitat choices: they home to the area used the previous year, but move on if that habitat is unsuitable" (Nichols 1996). Also, the tendency of adult birds to return to the previous year's breeding area is greater than the tendency of young birds to return to their natal area (Nichols 1996). Hourston (1959) has suggested the same tendency for BC herring.

With respect to trends in the metapopulation biomass, the first Factor of the principal component analysis defines the common, Regional pattern. Table 15 shows that this pattern explains 39% of the total variation in the metapopulation biomass. The rest of the variance (61%) is caused differences in the local response of the five major populations to changes in ocean climate and ecosystem structure. Fig. 17 indicates that the value of the second Factor has been particularly large since about 1990. The negative correlation between Factor 2, which in turn is correlated with water temperatures, and the QCI and WCVI stocks is consistent with the observation that these two stocks declined during most of the warm regime. In contrast, the Strait of Georgia stock has the highest positive correlation (r=0.72) with Factor 2, which is consistent with the fact that this stock has been increasing since the mid-1980s (Fig. 18). As noted

in the previous paragraph, part of the increase of the Strait of Georgia stock may have been caused by a higher straying rate of herring from the WCVI.

Successful management of the herring resource in BC requires reasonably accurate forecasts of the prefishery biomass in the next fishing season (Schweigert 2003). For the forecasts to be accurate, the repeat spawners must have a high fidelity (homing) to the stock assessment Region where they spawned the previous season. Tagging data indicate that BC herring have a high fidelity (85% on average) at the large spatial scales of the stock assessment areas (Hay et al 2001). However, at the much smaller spatial scales of the sections the fidelity rate averages only 17% (Hay et al 2001). We have also shown (Fig. 4,5,6, and 15) that at these small spatial-scales, there is considerable interannual variability in the abundance of spawners, presumably due to large variations in the number of adult herring straying between nearby sections from one spawning season to the next. This means that forecasts of herring biomass at the spatial-scale of the section would be far too inaccurate to manage the resource. The interannual straying rates of repeat spawners between sections is simply too high and erratic. Consequently, we conclude that the current stock assessment process, where the prefishery biomass is forecast for each of the five migratory stocks, and the 20% target harvest rate is removed from each major stock is the appropriate way to manage the resource. The current management policy has been successful because it spreads the harvest throughout the metapopulation, so it is proportional to the biomass of herring in each of the five major, component stocks. This policy also minimizes the potential over-harvesting of any small spatially discrete spawning aggregations (Schweigert 2003).

In closing, we emphasize that 34 sections have had continuous spawn records for the last 60 years (Appendix Table A3). These important sections contain about 85% of the total spawn habitat in BC, and therefore should be protected from shoreline development, pollution and other sources of habitat degradation. Loss of these habitats will almost certainly have a negative impact on the dynamics and resilience of the metapopulation.

Acknowledgements

This was a collaborative project between the Department of Fisheries and Oceans and the Herring Conservation and Research Society (HCRS). We are grateful to the HCRS for providing the funding to complete this project. We are also grateful to members of the PSARC Pelagic Subcommittee for providing constructive criticism of some of the ideas presented in this paper.

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Appendix

Table A1. Spawn length decline and recovery phases apparent in the sections with disappearance (DE) and recolonization (RCE) events. Some notable events in selected sections with continuous spawn records (i.e. no DEs) are also mentioned.

Region and (Section)	*Average Occupied length of spawn (km)*	*Phases and events apparent in the spawn time series*
QCI (6) Lousconne Inlet	5.6	No spawn recorded 1943-59. Erratic phase 1959-69. Rapid recovery 1970-1976. No DE's in record.
QCI (12) Naden Hbr.	7.6	No spawn recorded 1943-70. Possible recolonization event in 1970. Spawn recovery 1970-79. 1 DE, 0 RCE, currently vacant.
QCI (22) Skidegate Inlet	3.4	Spawn declined in 1987, DE=7 yrs (1989-95). unsuccessful recolonization in 1996. 2 DE's, 1 RCE, currently vacant.
QCI (23) Cumshewa Inlet	6.4	Long DE=23 yrs (1944-66), successful recolonization in 1967, spawn recovered in 5 yrs. Decline and sudden disappearance in 1996. 2 DE's, 1 RCE, currently vacant.
QCI (24) Laskeek Bay	6.6	Decline, long erratic phase from 1951-75, but no DE. Recovery began in 1976 and spawn length reached "equilibrium" in 6 yrs. No DE's in record.
QCI (25) Skincuttle Inlet	11.4	Spawn declined in early 1960s. Low abundance 1965-69, but no DE. Spawn recovered in about 5 yrs. No DE's in record.
PRD (43) N. Porcher Is.	5.0	Decline (1954-56), erratic (1957-62), DE=6 yrs (1963-68). Recolonization in 1969. Spawn length took 15 yrs to reach "equilibrium" (12 km). 1 DE, 1 RCE in record.
PRD (51) Banks Is.	2.3	Entire record is erratic. Five DEs and five unsuccessful recolonization events occurred. 5 DE's and 5 RCE's in record.
PRD (53) Principe Ch.	3.2	No spawn recorded 1943-55. Record erratic after 1955: 3 DE's and 3 RCE's. Most recent recolonization attempt in 2002, after 8-yr DE.
CC (62) Gil Island	8.7	Erratic record: 4 DE's and 3 RCE's, currently vacant. Last recolonization attempt in 1999.
CC (66) Surf Inlet	3.6	Record became very erratic after 1951. 4 DE's and 4 unsuccessful recolonization attempts between 1951-2002.
CC (72) Powell Anch.	17.8	Amount of spawn below average from 1946-81. Above average after 1982. No DE's in record.

Region and (Section)	*Average Occupied length of spawn (km)*	*Phases and events apparent in the spawn time series*
CC (73) Bella Bella	6.2	Zero entries appear after 1969, none before. 3 DE's and 3 RCE's in record. Amount of spawn above average from 1943-69. Spawn well below average 1970-on. *Possible movement of spawners from Section 73 to 72?*
CC (75) McNaughton Group.	3.0	Erratic spawn record except between 1972-84. DE=6 yrs (1955-60). Slow, erratic recovery; spawn length took 17 yrs to reach "equilibrium" (7 km). 1 DE and 1 RCE (1961) in record.
CC (77) Milbanke Sound	9.9	No spawn recorded before 1984. Six km of spawn appeared suddenly in 1984. Spawn length reached "equilibrium" (10 km) in 6 tears. No DE's in record.
CC (78) Spiller & Mathieson Ch.	16.3	Decline 1943-45, erratic phase (1946-51), one long DE=28 yrs (1952-79). Successful recolonization in 1980. Spawn reached "equilibrium" (22 km) in 10 yrs.
CC (82) Dean Channel	9.6	Decline (1943-47), DE=7 yrs (1948-54), unsuccessful recolonization (1955), DE=11 yrs (1956-66). Successful recolonization in 1969. Fast recovery (4-yrs) to "equilibrium" (13 km). 4 DE's and 4 RCE's in record.
CC (83) Bentinck Arms	12.4	Decline (1943-47), long erratic phase (1948-62), DE=6 yrs (1963-68). Successful recolonization in 1969, very fast recovery (2 yrs) to "equilibrium" (15 km). 2 DE's and 2 RCE's in record.
CC (84) Burke Ch.	13.9	No spawn recorded 1943-54. Long erratic phase 1955-69. Spawn increased (1970-77). Decline in 1992, DE in 1998, currently vacant.
CC (85) Kwakshua Ch.	10.1	Zero entries all before 1972, none after. No DEs in record.
CC (86) Fitzhugh Sound	2.3	Entire record is erratic. Spawn in this section appears to be continuously disappearing, and reappearing.
CC (92) Rivers In. Entr.	2.8	Possible DE in 1954. long erratic phase (14 yrs; 1980-93); one DE=6 yrs (1994-99). Recolonized in 2000.
CC (103) Smith Inlet	2.8	Erratic record: 3 DEs, 3 RCE's. Last recolonization attempt in 1998 was unsuccessful.
JS (112) Seymour Inlet & Nugent Snd	4.2	No spawn recorded 1943-49. Erratic phase (1950-66). Continuous spawn (1967-1981). Decline (1979-81), erratic phase (1982-89), one long DE (1990)=13 yrs, currently vacant.

Region and (Section)	*Average Occupied length of spawn (km)*	*Phases and events apparent in the spawn time series*
JS (123) W. Cracroft Is.	2.9	Mostly continous spawn 1943-77. Spawn declined (1973-77), long erratic phase (1978-94), DE in 1995, currently vacant. *Zero entries appear more frequently after 1977. Possible warm regime effect?*
JS (124) Wells Passage	2.8	Fairly continous spawn 1947-77. Erratic phase (1978-85), DE (1986)=10 yrs, unsuccessful recolonization attempt in 1996, DE (1997), currently vacant.
JS (133) Loughborough	1.5	No spawn reported from 1943-48. Possible DE in 1965. Spawn recovered. DE in 1984. Successful recolonization in 1990; recovery time = 10 yrs to "equilibrium" (3 km).
JS (135) Cape Mudge	3.2	Erratic (1943-58). Continuous spawn (1959-83). Erratic (1984-87). 1 DE (1988), 1 (or multiple) erratic recolonization events (1993-2002).
JS (136) Reed Island	0.6	Erratic spawning (1943-61). Section virtually vacant since 1962. Longest DE to date (35yrs). Very small amount of potential spawn habitat. Hence, section may not be surveyed very frequently. 2 DE's and 1 RCE, currently vacant.
GS (132) Deepwater Bay	1.5	Fairly continous spawn 1943-81 Decline 1982-87; possible DE in 1988. Long erratic phase 1988-2002.
GS (141) Oyster Bay	8.7	Virtually vacant from 1943-82. Erratic recolonization 1983-1994. Possible DE in 1995. Recolonization in 1999. 3 DE's and 3 RCE's in record.
GS (142) Baynes Sound	25.7	Gradual decline 1951-67. Possible DE in 1968. Recovery in 1971; spawn length increased for next 9 yrs.
GS (143) Qualicum	15.9	Gradual decline 1952-64. Possible DE in 1965; recovery in 1968; spawn length increased for next 8 yrs.
GS (152) Powell River	6.4	Decline 1985-90, erratic (1991-92), DE (1993)=5 yrs. Recolonization attempts in 1998 and 2000.
GS (162) Hotham Sound	1.4	DE= 7yrs from 1952-58. Successful recolonization 1959; recovery time = 2 yrs to K (1.5 km). Spawn decline 1972. Long DE=22 yrs began in 1978. 2 DE's, 2 RCE's in record. Last recolonization attempt in 2000. Section virtually vacant after 1978. *Warm regime effect?*

Region and (Section)	*Average Occupied length of spawn (km)*	*Phases and events apparent in the spawn time series*
GS (163) Malaspina St.	2.2	Continuous spawn 1943-1977. Decline began in 1970. Erratic phase and two DEs (1978-2002). Unsuccessful recolonization attempt in 1987; successful recolonization in 1996. 2 DE's and 2 RCE's in record.
GS (164) Jervis Inlet	2.7	Two DEs (1950 and 1979). Successful RE in 1958; recovery time = 1 yr to "equilibrium" (4 km). Spawn length declined 1976-78. long DE (1979) = 24 yrs, currently vacant. *Warm regime effect?*
GS (165) Sechelt Inlet	1.9	Continuous spawn 1943-72. Rest of record is erratic (1973-2002). Long DE (1988) = 12 yrs; recolonization attempt in 2000. *Warm regime effect?*
GS (172) Nanoose Bay	11.9	Continuous spawn 1947-84. Long decline began about 1975. Probable DE in 1988 (see text above). Successful recolonization in 1992. Spawn length increased, taking 9 yrs to reach "equilibrium" (26 km).
GS (181) Swanson Chan.	7.5	Continuous spawn 1943-83. Spawn declined from 1976-83. Record is erratic after that, but no DEs. *Warm regime effect?*
GS (182) Plumper Sound	2.1	Continuous spawn 1963-1982. Spawn declined 1974-82. Long DE=20 yrs began in 1983. Section currently vacant. *Warm regime effect?*
GS (191) Saanich Inlet	2.0	Mostly continuous spawn (1945-72). Sudden, long DE lasting 20 yrs began in 1973. Unsuccessful recolonization in 1993, followed by DE=6 yrs. Significant recolonization attempts (spawn lengths 5.6-8.3 kms) in 2000,2001,2002. 2 DE's and 2 RCE's in record.
GS (193) Victoria Hbr	0.4	Very small amount of potential spawn habitat. Erratic record with 4 DEs and 3 recolonization attempts, currently vacant.
GS (280) Howe Sound	1.8	No spawn reported 1943-1957. Continuous spawn 1960-68. long (17 yr) DE occurred in 1975. Erratic recolonization (or multiple attempts) began in 1992. Modest expansion still in progress.
GS (293) Boundary Bay	6.1	No spawn reported 1943-55. Decline, long erratic phase 1979-92, DE (1993) = 10 yrs, currently vacant. *Warm regime effect?*

Region and (Section)	*Average Occupied length of spawn (km)*	*Phases and events apparent in the spawn time series*
WCVI (231) Trevor Ch.	1.6	Continuous spawn 1943-62. Long erratic phase 1963-79. Sudden DE in 1979 which lasted 5 yrs. Unsuccessful recolonization 1985, last DE in 1986. 2 DE's, 1 RCE, section currently vacant (for 15 yrs). *Warm regime effect?*
WCVI (233) Imperial Eagle	1.5	Mostly continuous spawn 1943-62. Record erratic from 1963-2002, with 3 DE's and 3 RCE's. Latest recolonization attempt in 2001.
WCVI (241) Tofino Inlet	1.2	Continous spawn 1949-69. Virtually no spawn since then. Two DE's, one unsuccessful recolonization atempt in 1981. Currently vacant, current DE=21 yrs.
WCVI (242) Hesquiat Hbr.	4.2	Decline (1945-47); one DE in 1948 which lasted 11 yrs. Successful recolonization in 1959. Spawn length increased very slowly for next 42-yrs before reaching "equilibrium" (8 km). *Spawn lengths were mostly above average in this section from 1985-2000. Positive warm regime effect?* No spawning in this section in 2001 or 2002.
WCVI (251) Tahsis Inlet	0.7	Small amount of potential spawn habitat. Very erratic record, with 3 DEs and 2 unsuccessful recolonization attempts. Currently vacant for 31 yrs. Section is remote and therefore may not be surveyed regularly.
WCVI (252) Nootka Sound	4.6	Continuous spawn 1943-1977. Spawn erratic since 1978, but no DE's. *Warm regime effect?*
WCVI (262) Clannick Cove	2.1	Continuous spawn 1943-77. Spawn declined 1943-77. Sudden disappearance in 1977. Long DE=20 yrs began in 1978. Successful recolonization in 1998. *Good example of probable warm regime effect.*
WCVI (263) Checleset Bay	1.1	Mostly continuous spawn 1943-1965. Erratic 1966-75. Long DE=23 yrs began in 1976, currently vacant. *Warm regime effect?*
WCVI (272) Brooks Bay	4.0	No DE's greater than 4 yrs in record. However, three runs of zero entries lasting 4 yrs in the record suggest that DEs and recolonization events may be occurring regularly in this section.
WCVI (274) Holberg Inlet	0.8	Erratic spawns (1953-78). Spawn disappeared in 1979. *Warm regime effect?* 2 DE's, 1 RCE, currently vacant for 24 yrs.

Appendix Table A2. Logistic parameters describing the increase in spawn length during recovery and recolonization events. The Group 1 sections have *"continuous"* spawn records (i.e. no disappearance events, see Table A3). Most of these sections are in the main spawning area in each stock assessment region. The Group 2 sections have experienced one or more disappearance events. For Group 1 the tabulated spawn increase parameters were estimated for the late-1960s to early 1980s period. During the mid-1960s an intense herring reduction fishery depleted herring along the coast. Herring that spawn in the major stock assessment sections began to recover in the late-1960s and 1970s in response to the closure of the fishery (1968-71) and the lower harvest rates that were introduced when the "new" roe fishery reopened in the early 1970s. Note that [r] is the maximum exponential rate of increase in spawn, K is the "equilibrium" spawn length for the indicated period, and B is the scaled size of the spawn length at time zero. For the Group 2 sections, the spawn increase parameters were estimated during a period when these sections were being recolonized. For both Groups the recovery time indicates the number of years required for the spawn length to reach "equilibrium" after the initial recolonization. The "r" estimates for Dean Channel and Bentinck Arms are anomalously large, indicating that either the spawn record is suspect, or that there was an extremely large immigration of colonists from other sections during this period.

Section	K (km of spawn)	Period	B	r	Recovery time (yrs)
Group 1					
Louscoone Inlet (6)	14	1967-1978	4.9 E03	1.56	6
Laskeek Bay (24)	14	1975-1985	3.7 E01	0.58	6
Skincuttle Inlet (25)	20	1967-1984	8.2 E02	0.96	10
Pt. Simpson (33)	9	1964-1974	3.7 E06	3.09	5
Prince Rupert (42)	9	1969-1980	5.5 E01	1.83	6
Kitkatla Inlet (52)	17	1969-1984	4.6 E00	0.26	15
Kitasu (67)	18	1965-1979	3.4 E00	0.29	10
Powell Anch. (72)	6	1966-1980	1.5 E01	0.73	9
Thompson Bay (74)	15	1966-1980	1.9 E01	0.54	10
Kildidt Sound (76)	10	1965-1979	8.8 E00	0.40	9
Kwakshua Ch. (85)	13	1969-1981	3.7 E05	3.08	4
Rivers Inlet Head (93)	36	1963-1978	1.2 E01	0.32	10
Takush Hbr (102)	5	1962-1982	3.7 E00	0.71	8
Beaver Hbr (122)	6	1962-1972	3.6 E01	0.80	6
Thompson Snd (125)	6	1963-1977	3.5 E02	0.82	8
Kingcome Inlet (126)	17	1965-1982	5.9 E03	2.10	5
Knight Inlet (127)	18	1963-1978	9.7 E01	1.12	6
Bute Inlet (134)	13	1968-198	1.5 E02	2.85	3
Baynes Sound (142)	32	1970-1987	3.6 E02	0.82	10
Qualicum (143)	24	1970-1981	1.8 E04	1.85	6
Nanoose Bay (172)	20	1966-1980	1.0 E02	1.22	4
Yellow Point (173)	25	1967-1987	1.1 E02	0.66	11
Swanson Chan. (181)	19	1962-1975	4.4 E05	1.98	7
W. Barkley Snd (232)	19	1967-1987	6.8 E01	1.76	3
Sydney Inlet (243)	2.5	1967-1976	6.4	1.08	3
Vargas Is. (245)	12	1967-1981	3.5 E01	0.80	8
Nootka Sound (252)	7	1969-76	*	*	1
Esperanza Inlet (253)	10	1963-88	4.7	0.24	14
Forward Inlet (273)	9	1966-1991	1.9 E08	1.67	12
Group 2					
N.Porcher (43)	12	1968-1988	1.5 E01	0.26	15
McNaughton Grp (75)	7	1960-1982	4.1 E03	0.61	17
Milbanke Sound (77)	10	1983-2002	1.2 E01	0.81	6
Spiller Channel (78)	22	1979-2002	3.0 E02	0.65	10
Dean Channel (82)	13	1966-1976	*	***5.06***	4
Bentinck Arms (83)	15	1968-1990	*	***16.74***	2
Loughborough Inlet (133)	3	1989-2002	2.1 E05	1.26	10
Hotham Sound (162)	2	1958-1972	1.32	0.14	2
Jervis Inlet (164)	3	1957-1970	*	*	
Nanoose Bay (172)	26	1991-2002	6.0 E01	0.57	9
Hesquiat Hbr (242)	8	1958-2002	7.5 E01	0.17	ca. 40

Appendix Table A3. Locations of the 34 sections with "continuous" spawn records (i.e. no runs of zero entries in the time series longer than 4 years, see Methods).

Region	Major Stock Section	Minor Stock Section
Queen Charlotte Islands	6, 21, 24, 25	
Prince Rupert District	33, 42, 52	
Central Coast	67, 72, 74, 76, (77)[1], 85	93, 102
Johnstone Strait		122, 125, 126, 127, 134,
Georgia Strait	132, 142, 143, 172, 173, 181	
West Coast Vancouver Island	232, 243, 244, 245, 252, 253	272, 273

1. Continuous record since 1984.

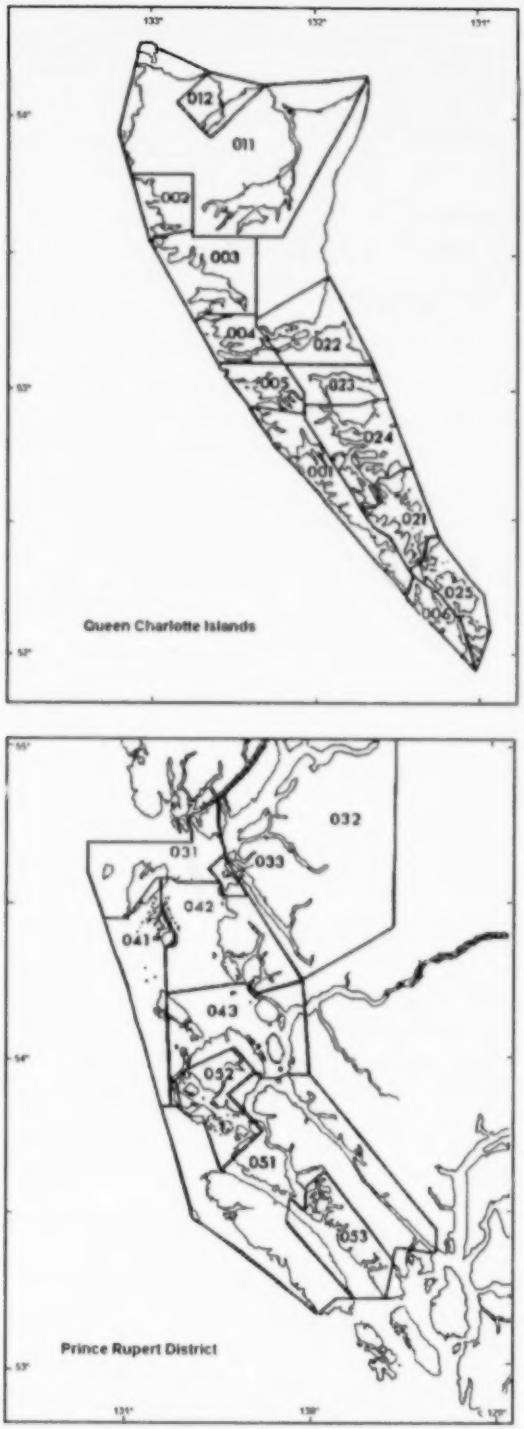


Figure 1. Herring sections in the Queen Charlotte Islands and Prince Rupert District Regions.

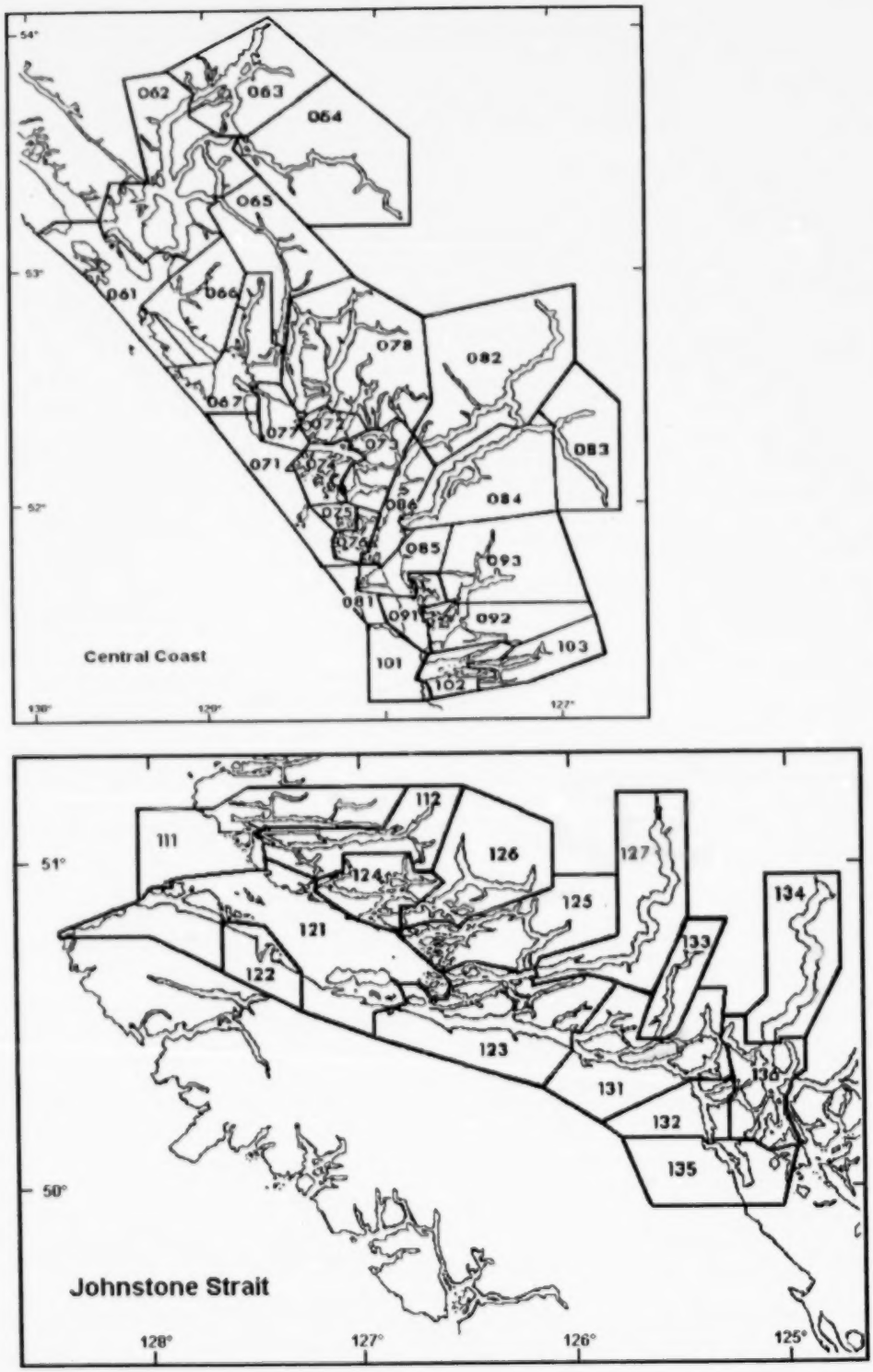


Figure 2. Herring sections in the Central Coast and Johnstone Strait Regions.

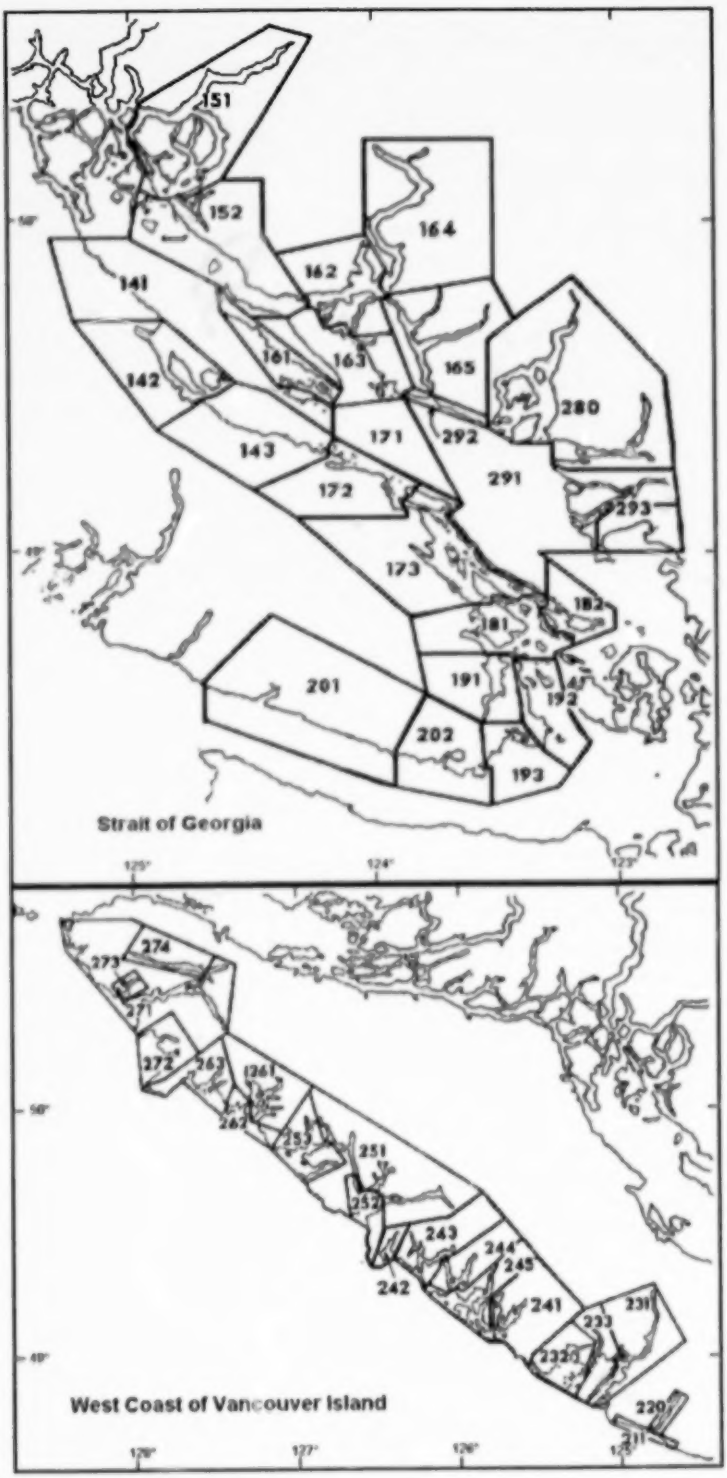
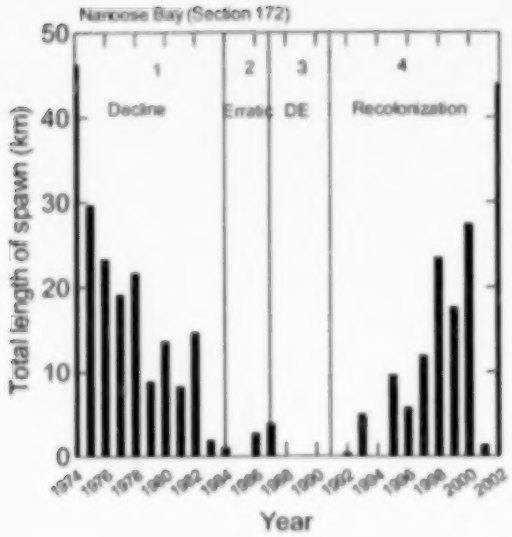


Figure 3. Herring sections in the Strait of Georgia and West Coast of Vancouver Island Regions.



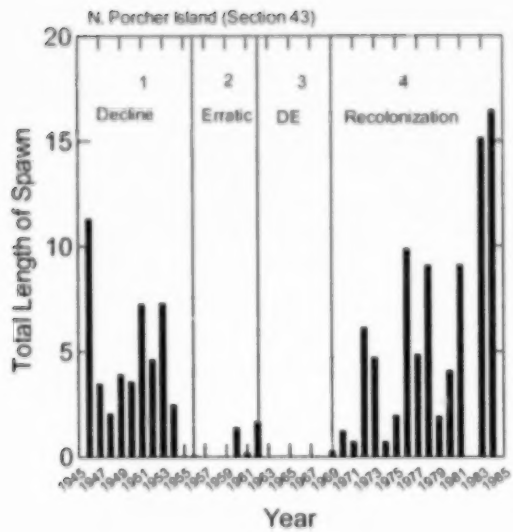


Figure 4. Examples of disappearance (DE) and recolonization events in the Nanoose Bay and N. Porcher Island Sections. These events occurred in four phases.

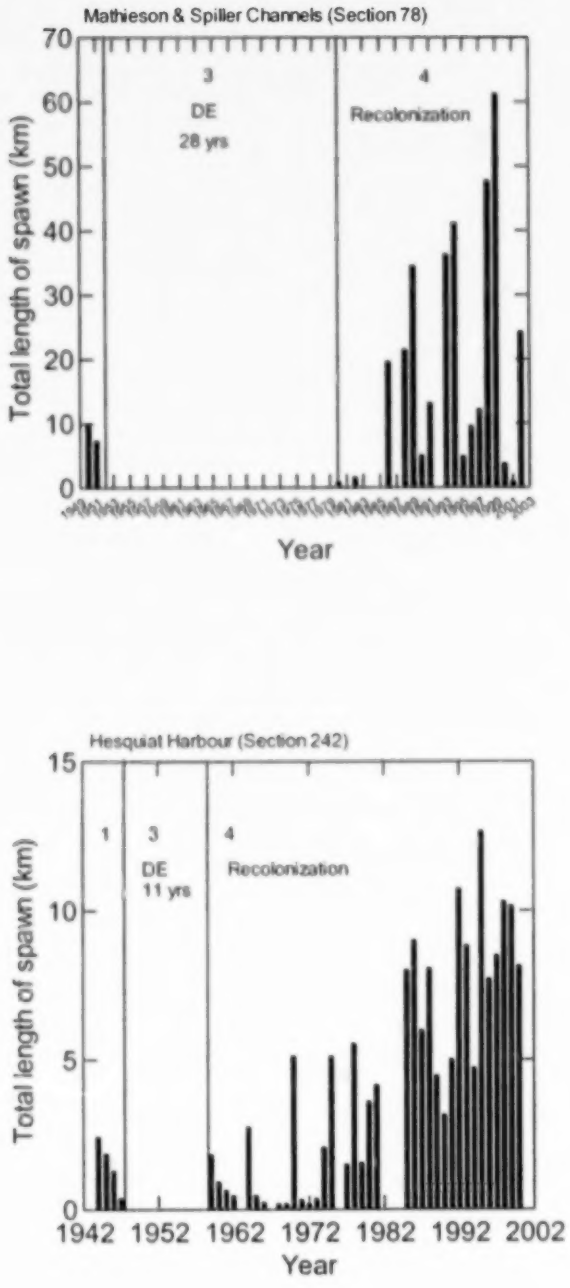
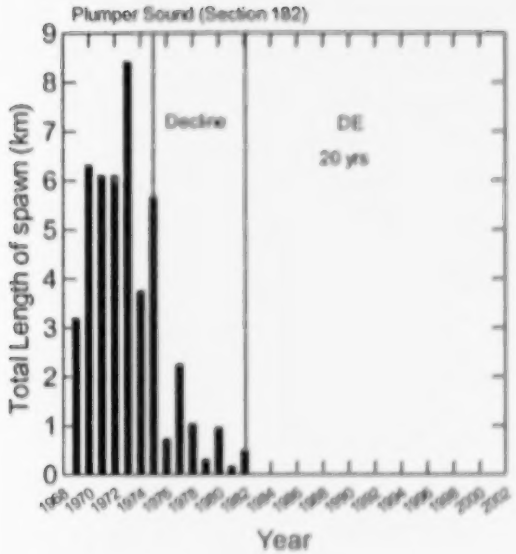


Figure 5. More examples of disappearance (DE) and recolonization events in Mathieson/Spiller Channels and Hesquiat Harbour Sections. There is no "erratic" phase (2) in these examples.



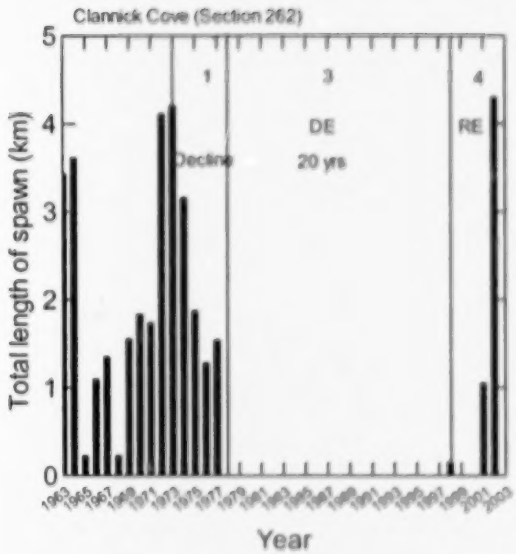
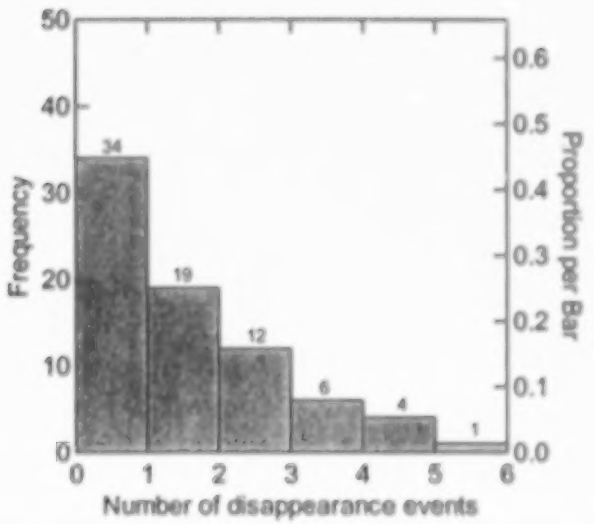


Figure 6 . Examples of two long disappearance (DE) events that may be associated with the transition to the warm climate regime in 1977.



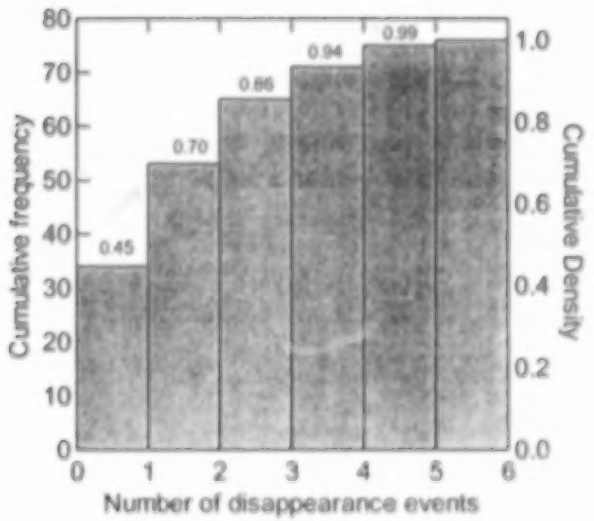


Figure 7. Frequency and cumulative frequency of disappearance events in the 76 Section database.

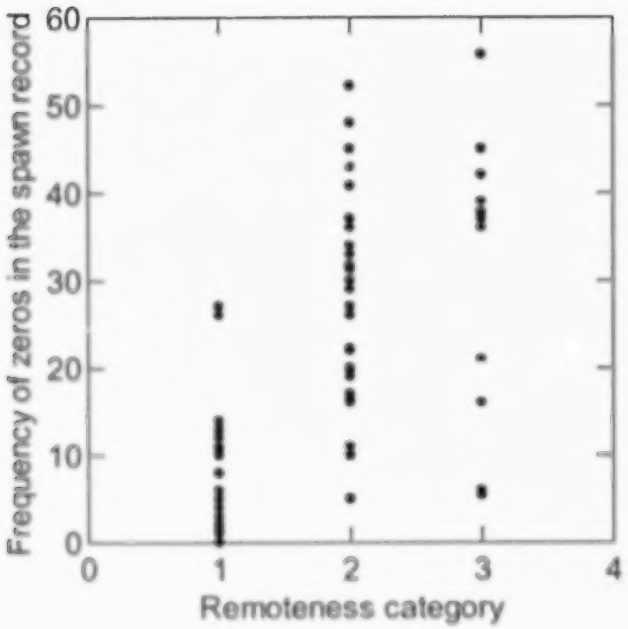
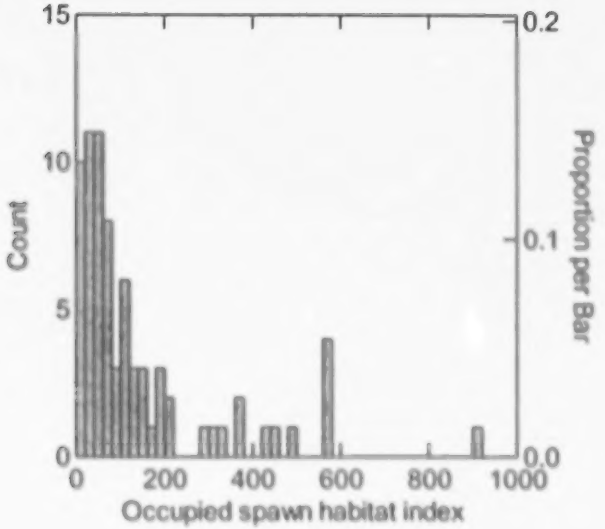


Figure 8. Frequency of zeros in the spawn records of the 76 Sections with respect to their relative remoteness from the main spawning area in each Region. Category 1 sections are in the main spawning area; category 2 sections are a little outside the main spawning areas, but along the outer coast; category 3 sections occupy the midsections and heads of long coastal inlets and, therefore, are the most remote (see Figs 1-3, and text).



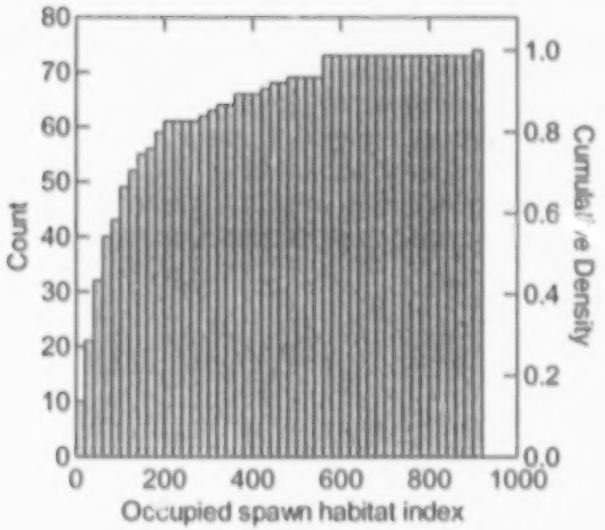


Figure 9. Frequency and cumulative frequency of the average occupied spawn habitat index (in thousands of units) in the 76 sections. Two cases with O-SHI indices > 1000 thousand units are not shown.

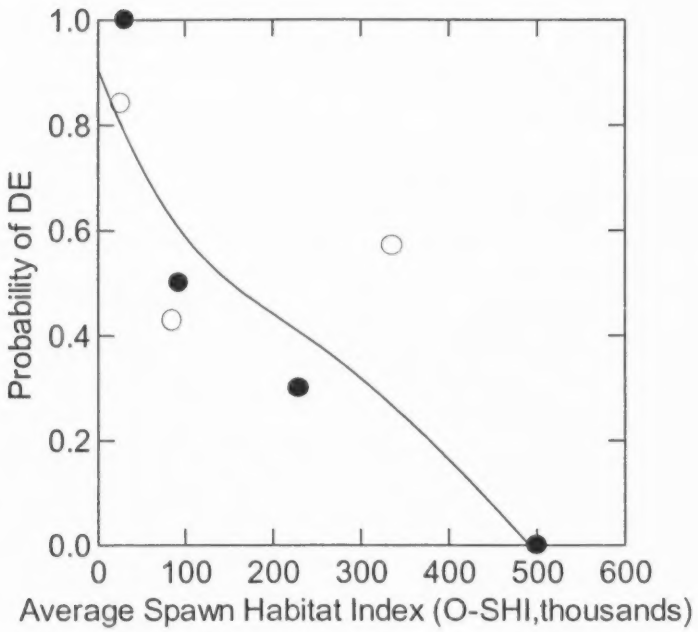
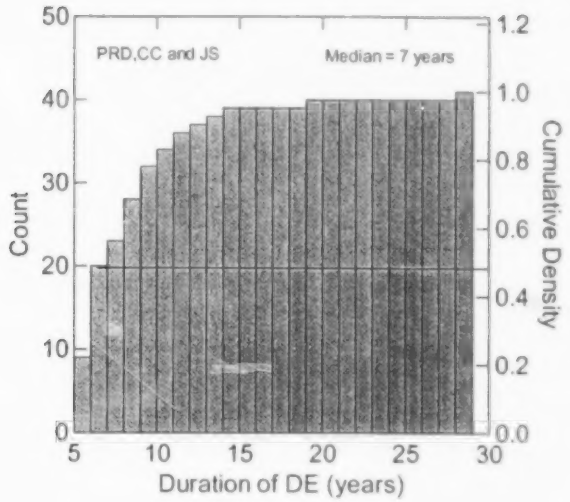


Figure 10. Relationship between the conditional disappearance event probability and the average amount of spawn habitat (O-SHI). Note that there is still a relatively high probability of disappearance events in mid-sized and large sections. There were no disappearance events in the very large sections which contain more than 500 thousand spawn habitat units. The solid circles indicate the probabilities for the Northern sections, and the open circles for the three Southern sections. The curved line indicates the smoothed coastwide trend.



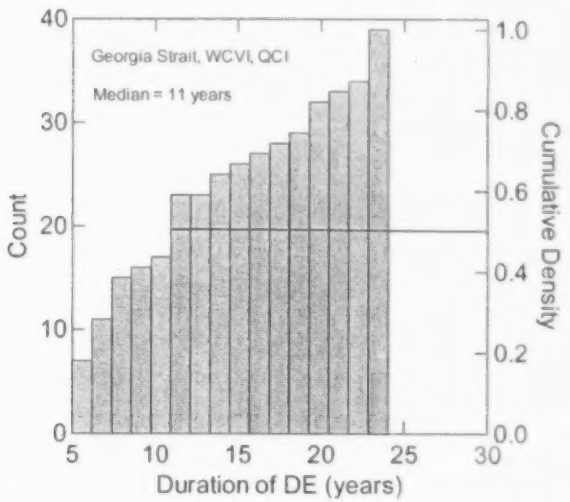
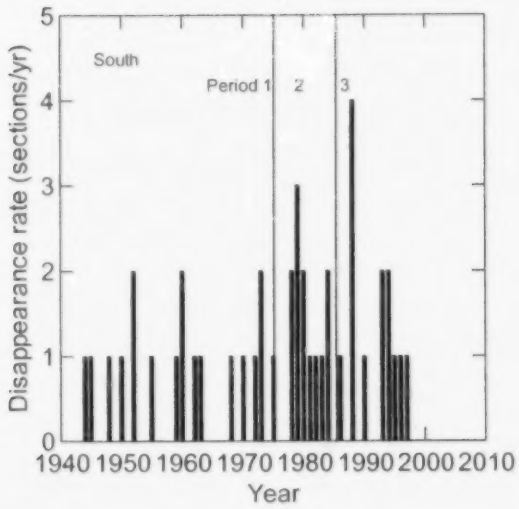


Figure 11. Cumulative frequency distributions of disappearance event duration (years) in PRD, CC and JS (median DE = 7 years); and in Georgia Strait, WCVI and QCI (median DE= 11 years).



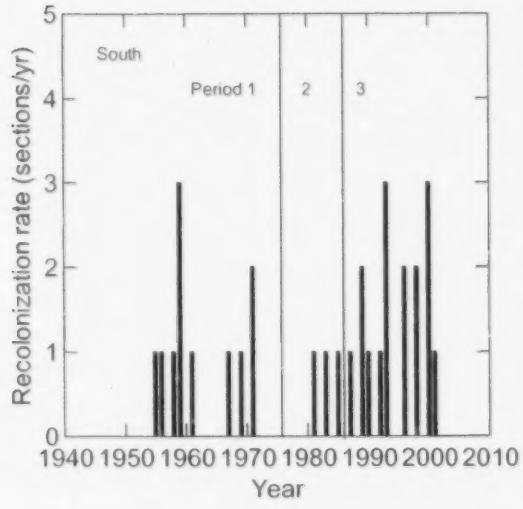
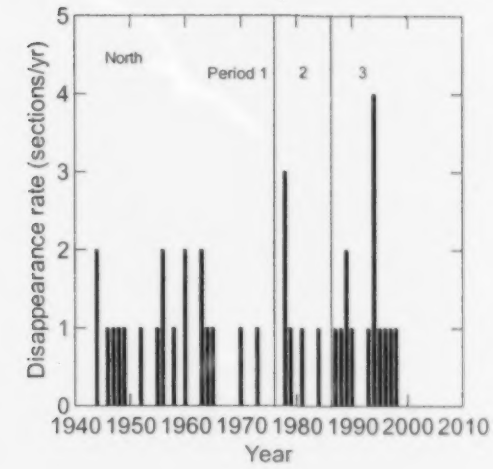


Figure 12. Disappearance and recolonization rate (sections/yr) time series in the three Southern Regions (JS,GS and WCVI). Three time periods where significant changes occurred are indicated (see text for explanation).



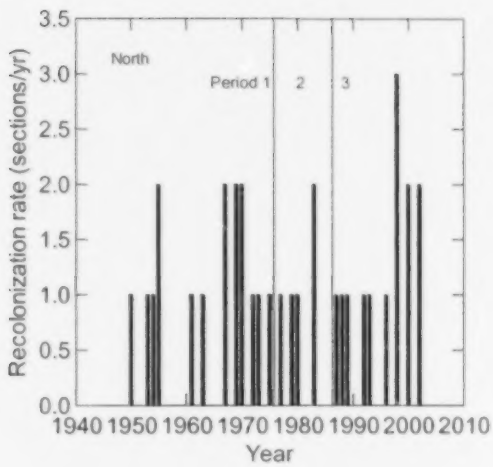


Figure 13. Disappearance and recolonization rate (sections/yr) time series in the three Northern Regions (PRD,QCI and CC). Three time periods where significant changes occurred are indicated (see text for explanation).

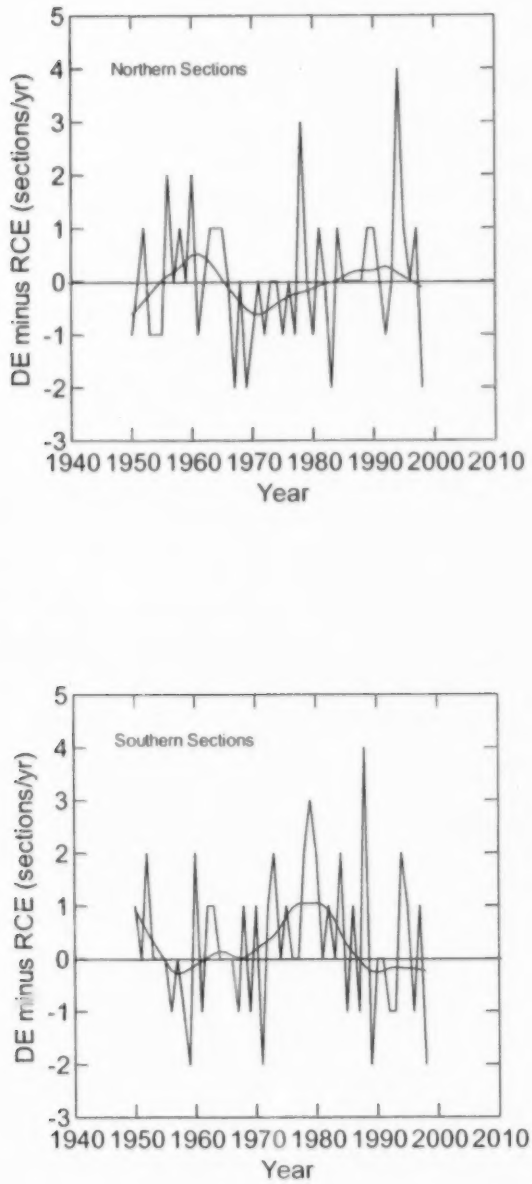


Figure 14. Annual difference between the disappearance (DE) and recolonization (RCE) rates in the three Northern (Top panel) and three Southern Regions (bottom panel).

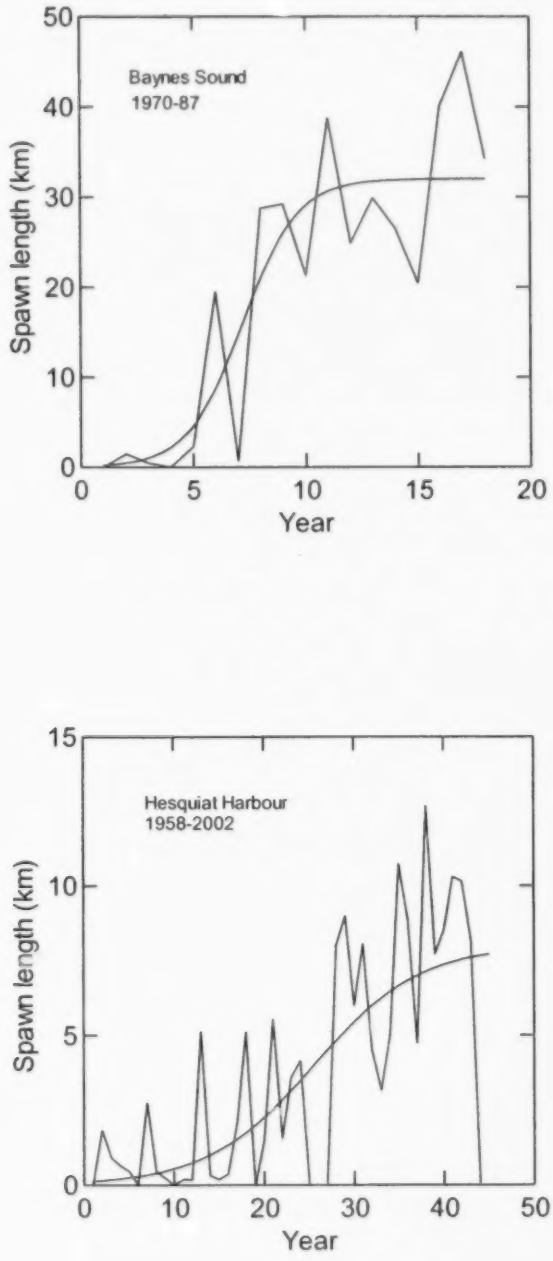
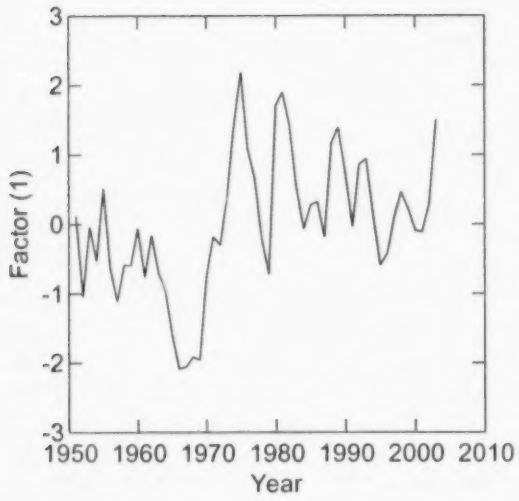


Figure 15. Logistic recovery rates in Baynes Sound and Hesquiat Harbour during two successful recolonizations. Note that the Baynes Sound group reached "equilibrium" in about 10 yrs, while the Hesquiat Harbour group required about 40 years.



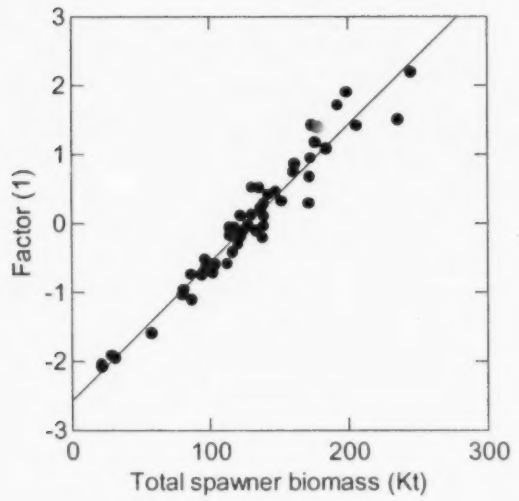
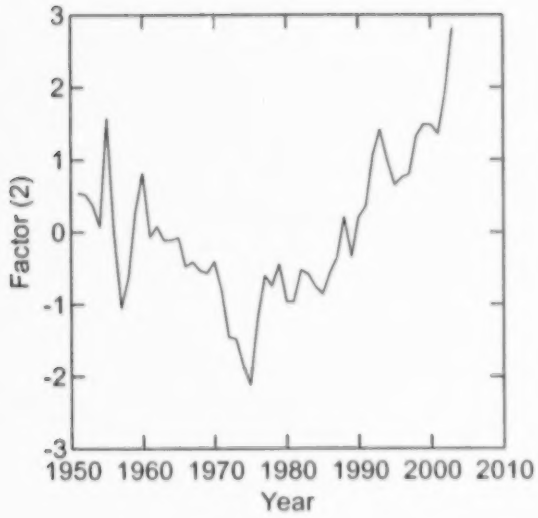


Figure 16. The regional pattern in spawner biomass in the metapopulation is defined by the Factor (1) time series (top panel). Factor (1) is highly correlated with the total estimated spawner biomass (bottom panel; $r = 0.97$; $n = 53$; $p < 0.0001$).



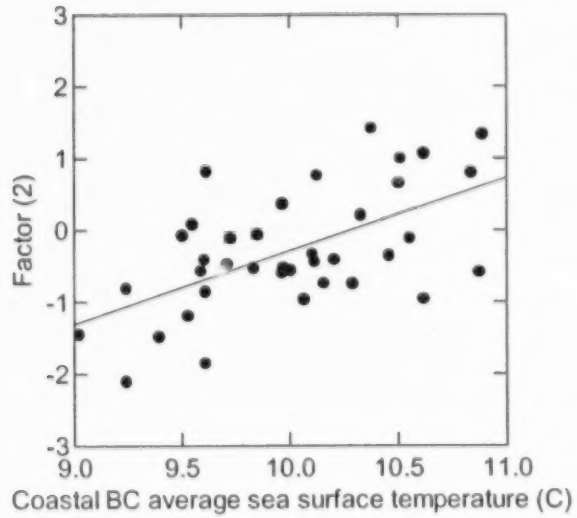


Figure 17. Factor (2) time series (top panel). Factor (2) is correlated with the annual SST along the BC coast since 1960 (r = 0.58; n = 39; p = 0.0001).

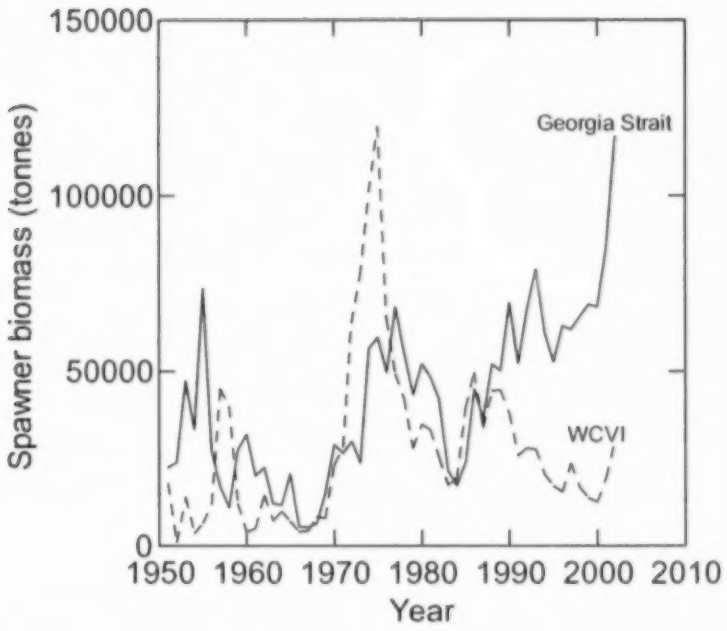


Figure 18. Spawner biomass time series for the West Coast of Vancouver Island, and Georgia Strait populations, as estimated by the age-structured model (Schweigert 2003). These populations began drifting out-of-phase around 1989.